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BULLETIN OF MARINE SCIENCE OF THE GULF AND CARIBBEAN

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THE PHYLLOSOMA LARVAE OF THE SPINY LOBSTER *PANULIRUS ARGUS*[1]

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ABSTRACT

THE PHYLLOSOMA LARVAE of the spiny lobster, *Panulirus argus* (Latreille), were obtained from plankton hauls made in the western Atlantic and Caribbean. Eleven stages were identified of which the last is probably the final stage before metamorphosis. Stage one was obtained from freshly hatched eggs. It was shown that the larvae may be carried long distances by currents and that some of the larvae taken off the Florida coast were hatched much farther south.

INTRODUCTION

Panulirus argus (Latreille) is the common spiny lobster of Florida and of parts of the Caribbean. The adults are found under rocks and ledges along the coast of the western Atlantic from Brazil to North Carolina and about the islands of the West Indies. It is chiefly in Florida, Bahamas, Bermuda and Cuba, however, that they are caught in sufficient numbers for commercial exploitation (Smith, 1948; see also Gruvel, 1912).

The phyllosoma larvae of the spiny lobster are flat, transparent animals, greatly modified for a planktonic existence. Although a few stragglers are to be found throughout the year, the bulk of the larvae are found in the summer and early winter months, drifting northward in the waters of the Florida Current. These larvae pass through successive moults and, at least in the Miami area, reach the last stages of larval development in January or February. The larvae then metamorphose and the first puerulus, adult in form but transparent and with a few red pigment spots, collect under rocks and crevices along the shore.

The newly hatched phyllosomas of *Panulirus argus* were first obtained by Crawford and DeSmidt (1922) but their figure gives little detail. The first stage was more fully described by Lebour (1950)

1 Contribution No. 52 from The Marine Laboratory, University of Miami.

from specimens hatched in the Bermuda Aquarium and stage three was described by the same author from a specimen taken in a net haul in the Atlantic off Bermuda. Later stages of the genus were described by Gurney (1936). However, as the early stages were then lacking, positive identification of his species was not yet possible.

Gilchrist (1913, 1916) described a pre-phyllosoma stage in *Palinurus* (*Jasus*) *lalandii,* a related genus. He named this "naupliosoma" and commented that it lasted only a few hours and might easily be missed if hatching occurred during the night, since the first phyllosoma stage would have been reached by morning. Von Bonde (1936) showed that there was a pre-naupliosoma stage in this species which lasted for about eight hours before moulting into the naupliosoma stage. Sheard (1949) records a naupliosoma stage in *Panulirus longipes.* Neither of these stages was seen by either Lebour (1950) or the author. The eggs of *Panulirus argus* hatch as first phyllosomas.

Some 300 specimens, excluding freshly hatched specimens from a berried female, compose the material on which the present study is based. Of these, a few belong to the genera *Scyllarus* and *Thenus* and some to species of *Panulirus* other than *argus.* The bulk of the material was identified as *Panulirus argus.* The first stage is described from freshly hatched larvae from a berried female and the subsequent stages follow such a logical sequence of development that there can be little doubt of their identification. Although none of the larval stages of *Panulirus argus* have been directly linked by observation before and after moulting, the quantity of material available left little likelihood of any stages being missed except, possibly, the final one.

The material was obtained from plankton hauls made for Dr. Hilary B. Moore by the Woods Hole Oceanographic Institution vessel "Atlantis" in the western Atlantic and the Caribbean and from hauls made from the oceanographic vessels of the Marine Laboratory, University of Miami, in the waters of the Florida Current off Miami. Hauls were made with a 70 cm. diameter net, grading from a lead mesh of ¼ inch, through a stramin section, to a cod-end of No. 10 silk. Tows usually covered about one mile. Those from the "Atlantis" were mostly made at the surface about midnight, while the Miami hauls were mainly made in the daytime over a range of depths. As yet there are inadequate data from which to draw any conclusions on the vertical distribution of the larvae. It may be noted that none was taken at any time in numerous tows made in coastal waters inside Biscayne Bay.

My thanks are due to Dr. F. G. Walton Smith, Director of the Marine Laboratory, for his kind permission to use the facilities of the Marine Laboratory; to Dr. Hilary B. Moore, both for his encouragement and helpful criticism and for making available the data and material obtained in investigations sponsored by the National Geographic Society; to William Babis for his data on material from the "Atlantis" hauls; and to Dr. W. L. Schmitt and Dr. F. A. Chace for helpful criticism of this manuscript.

The Phyllosoma Larval Stages

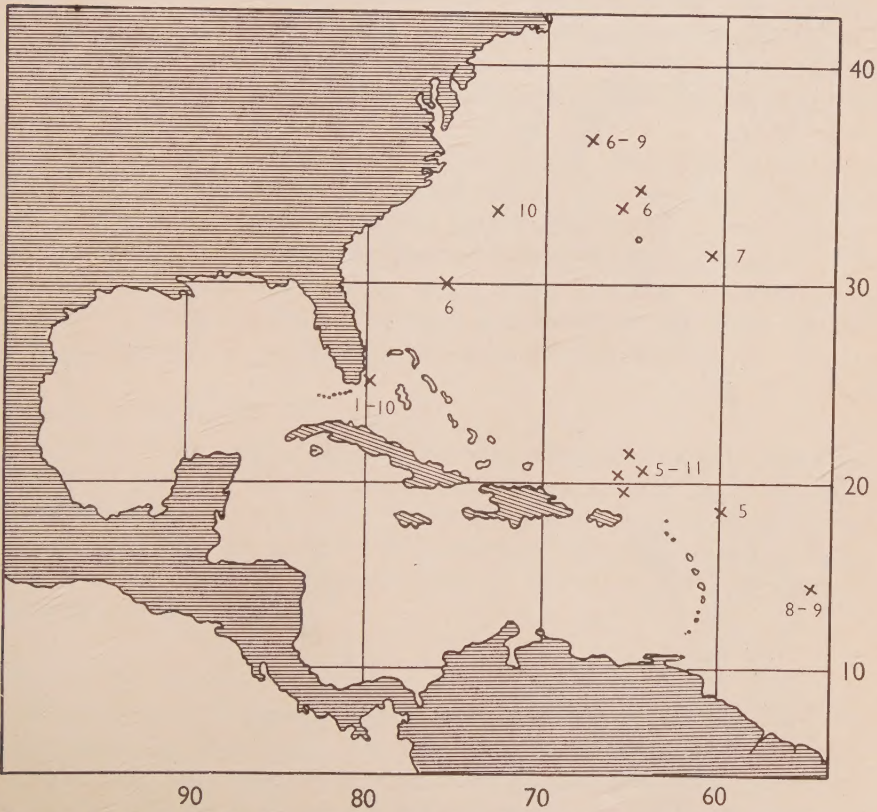

Figure 1. Map of the West Indies showing the stations at which phyllosomas of *Panulirus argus* were taken in net hauls. The stations are indicated by *X*; the figures indicate the stages of the larvae taken at each station.

Stage 1. Figures 2A, 5A, B and I.

The fore-body of the cephalothorax is pear-shaped, rounded ante-

riorly and obtusely pointed posteriorly. The hind-body is roughly elliptical in shape, as long as, but narrower than the fore-body. The

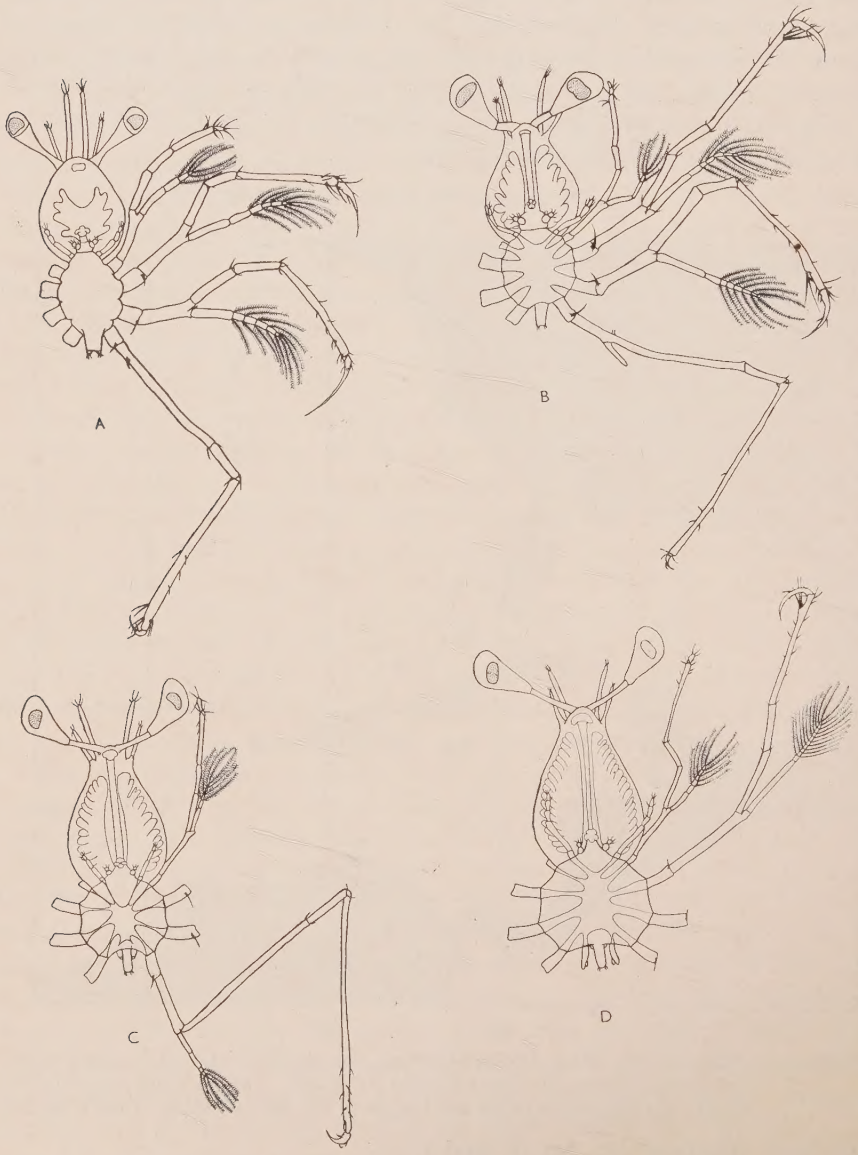

FIGURE 2. Phyllosomas of *Panulirus argus*. A, stage 1; B, stage 2; C, stage 3; D, stage 4. (ventral view throughout).

abdomen is unsegmented and is tipped by two round processes, each of which possesses four setae. The antennae are unsegmented and tipped with four setae. The antennules are longer than the antennae, unsegmented and tipped with three setae. Three pairs of legs are present. The first two pairs are biramous, while on the third, a small bud on the meral segment of the endopodite is the precursor of the exopodite. Coxal spines are present on all the legs. The eyes lack stalks.

There is a simple, triangular-shaped upper lip. The mandible consists of a basal portion and a distal portion ending in three tooth-like denticles. The first maxilla consists of a short basal part inserted immediately behind the mandible. It has two short branches, each provided with two long plumose setae and a pair of smaller setae. The shape and arrangement of the mandibles and maxillae do not alter markedly in later stages.

There is a flat and bladelike second maxilla consisting of two segments. The exopodite of the maxilla bears four setae and the base three. The first maxilliped bears a single spine and is a mere stump-like projection immediately behind the base of the second maxilla. The second maxilliped is tipped by three setae, lacks an exopodite and consists of four segments. The third maxilliped is very long and resembles the legs in appearance but lacks a coxal spine.

Stage 2. FIGURE 2B, 5C.

The fore-body is pear-shaped but more elongate than in stage one. The hind-body is rounded but is still narrower than the fore-body. Short stalks have appeared on the eyes but there is no marked change in the antennae, antennules or mouthparts from the form of stage one. The presumptive exopodite bud on the third leg has increased markedly in size.

Stage 3. FIGURE 2C.

The fore-body is more elongate than in stage two and only slightly wider than the hind-body. The abdomen is narrower than in stages one and two, and a pair of limb buds, one on each side of the abdomen, is present. There is a well-formed exopodite on the third leg. The antennae are still shorter than the antennules. Stage three of Lebour has no setae on the antennae but it is suggested that these may have been broken off as they were present on each of a half dozen or so specimens examined from the "Atlantis" material. The coxal segments of the three pairs of legs are longer and narrower relative to

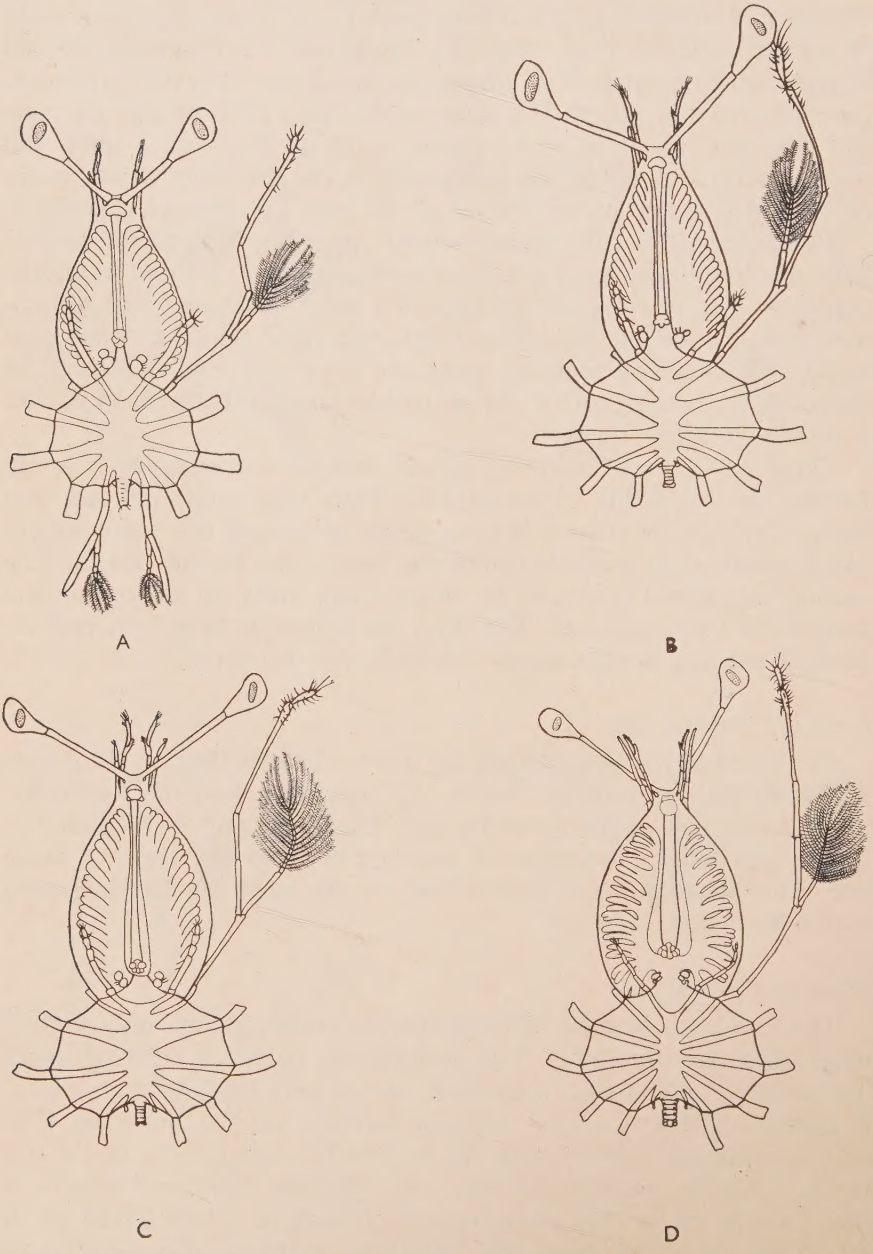

FIGURE 3. Phyllosomas of *Panulirus argus*. A, stage 5; B, stage 6; C, stage 7; D, stage 8.

the rest of the body than in either of the two previous stages. The eye stalks have increased in length.

Stage 4. FIGURES 2D, 5J.

The fore-body is only as wide as the hind-body and acutely pointed posteriorly. The antennae are still shorter than the antennules. The eye stalks are as long as the antennules. The hind-body bears an elongated pair of limb buds which are bifurcate at their tips, foreshadowing the final biramous nature of the fourth pair of legs. Closely applied to the abdomen is a new pair of limb buds representing the fifth pair of legs. The abdomen is narrow and without the apical setae.

Stage 5. FIGURES 3A, 5D.

The fore-body is not as wide as the hind-body and is narrow and sharply pointed posteriorly. The antennules have two segments and the antennae are only as long as the first segments of the antennules. The eye stalks are longer than the antennules. The fourth pair of legs has small setose exopodites and short endopodites tipped with fine setae. The limb buds of the fifth pair of legs are still rudimentary. Only a few specimens of this stage bear coxal spines while there is no evidence of coxal spines on the developing fourth pair of legs. Both the exopodite of the second maxilla and the first maxilliped have lost their setae. Three setae remain on the base of the second maxilla. There is a trace of segmentation in the abdomen.

Stage 6. FIGURES 3B, 5K.

The fore-body is long and narrower than the hind-body. The antennules have three segments and have a fringe of three setae along their median edge as well as a tuft of setae at the tip. The distal end of the second segment has a small protuberance on the median edge, tipped with a single seta. The antennae have two segments and are only as long as the first two segments of the antennules. The eye stalks are longer than the antennules. The fourth pair of legs is completely formed while the presumptive limb buds of the fifth pair of legs are still rudimentary. There are no coxal spines on any of the four pairs of legs. The adbomen is still small and narrow. It appears to have undergone no increase in size throughout the previous development.

Stage 7. FIGURES 3C, 5E and L.

The antennules have four segments. The tip of each has four setae and there is a fringe of setae along the median edge of the last seg-

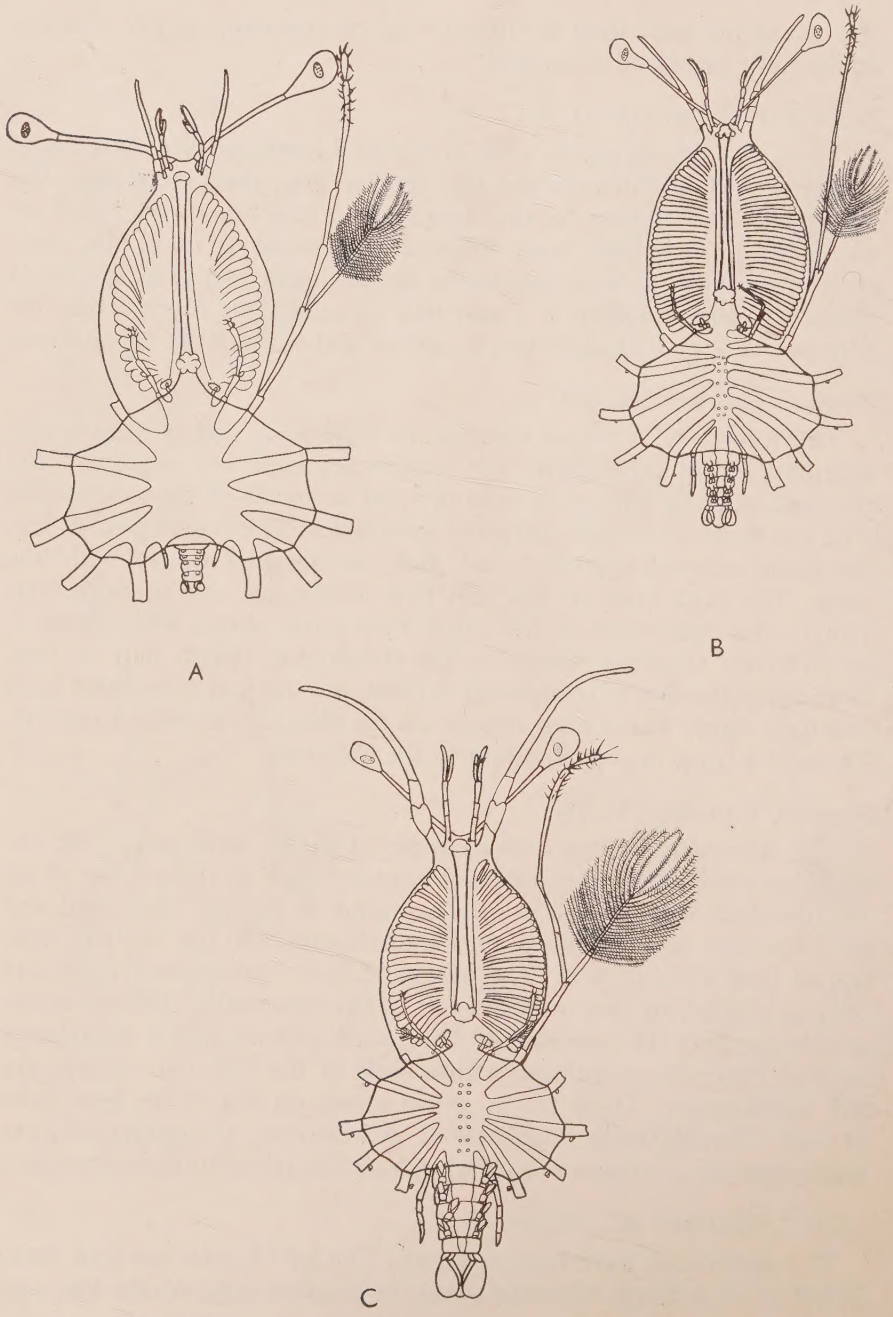

FIGURE 4. Phyllosomas of *Panulirus argus*. A, stage 9; B, stage 10; C, stage 11.

ment. The protuberance of the penultimate segment (the future endopodite of the antennule) has increased in length and bears three setae along its median edge. The antennae have three segments and are only as long as the first three segments of the antennules. The limb buds of the fifth pair of legs are no longer closely applied to the abdomen and are slightly elongated. The abdomen is markedly segmented and each segment bears a small pair of buds (the developing pleopods). The telson is only slightly developed.

Stage 8. FIGURES 3D, 5M and F.

The antennules have five segments and have lost the apical tuft of setae. There is, however, still a fringe of setae along the median edge of the last segment. The antennae have three segments, are as long as the antennules and have lost the setae of their tips. The eye stalks are almost twice as long as the antennules. There is a small and imperfectly formed telson. The buds of the fifth pair of legs have elongated slightly and are each composed of two segments. The second maxilla is very large and fringed with setae. The first maxilliped has increased in size and almost reaches the base of the exopodite of the second maxilla.

Stage 9. FIGURES 4A, 5N.

The antennae have four segments and are longer than the antennules but not as long as the eyes and eye stalks. The antennules are six-segmented with each lobe of the bilobed apex a distinct segment. The abdomen has four pairs of bilobed pleopod buds. The telson is small but almost perfectly formed. The legs of the fifth pair have two segments and are more elongate than in the previous stage. The exopodite of the second maxilla has increased in size. The first maxilliped is taller than the base of the second maxilla. The second maxilliped bears a presumptive exopodite bud.

Stage 10. FIGURES 4B, 5G and O.

The antennae are as long as the eyes and eye stalks combined. The second maxilliped has a partly formed exopodite bud. The coxae of the first four legs bear small gill buds. The fifth leg is composed of three segments. The abdomen bears bilobed pleopods and a well-formed telson. The exopodite of the second maxilla is longer than in the previous stage. The first maxilliped has differentiated into an epipodite, a long endopodite which does not quite reach the edge of the maxilla, and a small exopodite bud. The exopodite of the second

maxilliped is about half the length of the endopodite but lacks any setae.

Stage 11. FIGURES 4C, 5H and P.

The antennae are longer than the eyes and eye stalks, and show traces of segmentation on the apical flagella. The endopodites of the antennules are almost as long as the exopodites. The exopodites of the second maxillipeds are fully developed with setae. The first four

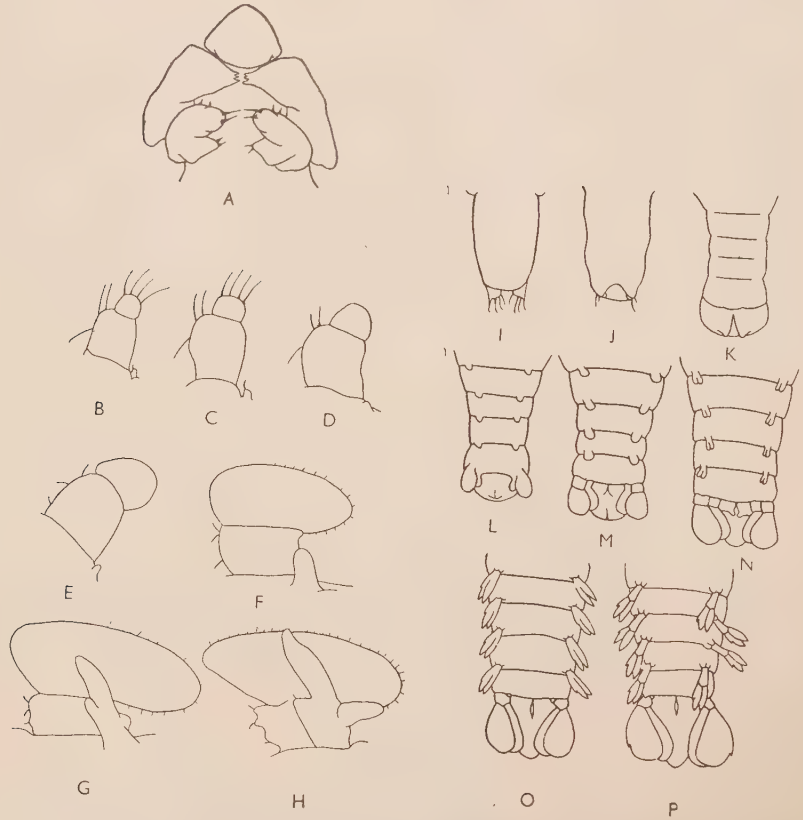

FIGURE 5. Mouthparts and abdomens of phyllosomas of *Panulirus argus*. A, upper lip, mandibles and first maxillae of stage 1; B, second maxilla and first maxilliped of stage 1; C, maxilla and maxilliped of stage 2; D, maxilla and maxilliped of stage 5; E, maxilla and maxilliped of stage 7; F, maxilla and maxilliped of stage 8; G, maxilla and maxilliped of stage 10; H, maxilla and maxilliped of stage 11; I, abdomen of stage 1; J, abdomen of stage 4; K to P, abdomens of stages 6 to 11, inclusive.

legs bear bilobed gills on the coxal segments. The fifth leg is composed of five segments. The abdomen bears a large, fully-developed telson while the pleopods are small but completely formed. The endopodite of the first maxilliped is larger and reaches the edge of the maxilla. The exopodite is about half the length of the endopodite.

Discussion

Of the 11 stages described, it is only in the first four that individuals of the same stage show no differences in size or degree of development. In the latter seven stages, however, there is considerable variation between individuals in the same stage. Thus the stages chosen represent the "average" state of development of specimens in each size group. The range of measurements for each stage is contained in Table 1.

TABLE 1
Measurements of Lengths (mm.) of Phyllosomas of *Panulirus argus*

Stage	No. Specimens Examined	Antennules	Antennae	Eye and Stalk	Abdomen	Thorax
1	5	0.5	0.4	0.6	0.2	1.4
2	5	0.7	0.5	1.1	0.3	1.9
3	5	0.8	0.5	1.2	0.4	2.8
4	5	0.9	0.6	1.6	0.5	3.6-4.1
5	10	1.0-1.1	0.6	2.0	0.5	4.8-5.5
6	10	1.3-1.6	0.8-1.1	2.8-3.9	0.5	6.4-8.3
7	10	1.7-1.9	1.0-1.3	3.7-4.3	0.5-0.6	8.0-9.5
8	10	2.1-3.0	1.9-3.4	5.2-6.6	0.8-1.6	10.9-13.0
9	5	3.0-3.4	3.7-4.4	6.5-7.0	2.0-3.2	14.0-16.1
10	3	3.7-3.9	6.5-8.5	7.2-7.8	4.0-5.4	16.7-17.8
11	3	4.8-5.2	11.5-13.4	7.7-8.8	6.6-7.8	17.7-19.6

Stages one and three correspond almost exactly with those of Lebour. The later stages do not correspond in every respect with those figured by Gurney. He suggested that his *Panulirus* B. is *Panulirus argus,* while *Panulirus* A. is *Panulirus regius*. The stages described in this paper resemble most closely those of Gurney's *Panulirus* B. but differ from them in some respects. The hind-body in stages 10 and 11 is not as much wider than the fore-body as in *Panulirus* B. and in the first three stages is narrower than the fore-body. The development of the antennae and antennules parallels that of *Panulirus* B. Coxal spines are lacking in the later stages as in *Panulirus* B. but are present in the first four stages. As in *Panulirus* B. the development of the exopodite of the maxilla does not begin until late (stage eight), but unlike *Panulirus* B. it bears setae from the beginning of its develop-

TABLE 2

SUMMARY OF THE CHARACTERISTICS OF PHYLLOSOMAS OF *P. argus*

Stage	Body Width Fore/Hind	Antenna / Antennule	Antenna / Eye Stalk	Antenna Segments	Antennule Segments	Abdomen
1	>1	<1	-	1	1	unseg.
2	>1	<1	>1	1	1	unseg.
3	>1	<1	1	1	1	unseg.
4	1	<1	<1	1	1	unseg.
5	<1	<1	<1	1	2	trace
6	<1	<1	<1	2	3	segt.
7	<1	<1	<1	2	4	segt.
8	<1	1	<1	3	5	segt.
9	<1	>1	<1	4	6	segt.
10	<1	2	>1	4	6	segt.
11	<1	>2	>1	4	6	segt.

ment. The setae are lost, however, in the intermediate stages and appear again with the differentiation of the maxilla in stage eight.

Stage 11 is probably the last phyllosoma stage before metamorphosis to a puerulus. It has reached the same state of development as stage 10 of Gurney's *Panulirus* A. which he considers the last larval stage. Again, stage 11 resembles the last larval stage of *Panulirus vulgaris* which was observed in the process of metamorphosis by Bouvier (1914).

TABLE 3

DEVELOPMENT OF THE LEGS IN PHYLLOSOMAS OF *P. argus*

Stage	First		Second		Third		Fourth		Fifth	
	Ex.	End.	Ex.	End.	Ex.	End.	Ex.	End.	Ex.	End.
1	+	+c	+	+c	b	+c	—	—	—	—
2	+	+c	+	+c	b	+c	—	—	—	—
3	+	+c	+	+c	+	+c	b	b	—	—
4	+	+c	+	+c	+	+c	b	b	b	b
5	+	+	+	+	+	+	+	i	b	b
6	+	+	+	+	+	+	+	+	b	b
7	+	+	+	+	+	+	+	+	b	b
8	+	+	+	+	+	+	+	+	i	i
9	+	+	+	+	+	+	+	+	i	i
10	+	+g	+	+g	+	+g	+	+g	i	i
11	+	+g	+	+g	+	+g	+	+g	i	i

+ = completely formed, b = bud, g = gill, c = coxal spine, i = incompletely formed, — = absent.

Tables 2 and 3 summarize the most important differences between the 11 stages. Table 2 shows the ratios between the width of the fore-body and hind-body, the ratios between the antennae, antennules and eye-stalks, and the numbers of segments of the antennae and anten-

nules for each stage. Table 3 shows the most important points in the development of the legs.

Adult Breeding Season and Distribution of Larvae

An account of the breeding habits of *Panulirus argus* in the Caribbean has been published by Smith (1948). In Florida the peak of the mating activity of *P. argus* occurs between February and April. During this period the male extrudes a viscous fluid from the swollen openings at the base of the last pair of legs. This fluid becomes attached to the under surface of the female between the last pair of legs and rapidly hardens on the outside to form a sac holding the sperm.

Shortly after mating, the female extrudes her eggs which become attached to the pleopods. The eggs are bright orange in color and about one mm. in diameter. Fertilization is accomplished when the spermatozoa are released from the soft inside of the sperm sac by scratching it with the tips of the legs of the female. There is rather a wide variation in the mating date, and as a result a small number of females may still be found with eggs as late as October. The spent sperm sac may remain attached in a few cases until late November.

The mating season probably occurs both earlier and later in warmer parts of the Caribbean. According to Smith (1948), female lobsters were found with sperm in the Bahamas chiefly between April and August but some females were to be found with sperm throughout the year. He also found that, at Glover's Reef, British Honduras, during October 1947, 60 per cent of breeding females carried eggs.

The larvae hatch out in two or three weeks and begin their planktonic existence. In the vicinity of Miami the bulk of the freshly hatched larvae appear in the plankton between June and August, although a few are taken as early as the latter part of April. The last larval stages were taken in hauls in December and January.

Between January and March the metamorphosed lobsters appear in inshore waters. These are the puerulus stage and they differ from the adults chiefly in the absence of any lime in their skeletons, in their transparency and in their lack of pigmentation. After several moults these reach a length of somewhat greater than one inch and acquire the color of the adults. A more detailed account of the growth and ecdysis of the puerulus and adult lobsters will be given in a later paper.

Table 4 summarizes the catches of each stage in the vicinity of Miami for 1950 and 1951, on the basis of the percentage of each monthly catch. While hauls were made frequently over a period from

TABLE 4

MONTHLY CATCHES OF *P. argus* FOR 1950, 1951 ON BASIS OF PER CENT OF TOTAL NUMBER CAUGHT

STAGE	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	JAN.	FEB.
1	100	100	19						
2			7						
3			30						
4			23	100	33				
5			16						
6					33		36	33	
7					33		57	16	
8							7	33	
9									
10								16	
11									
Total	1	2	28	2	3	0	14	6	0
No. Hauls	1	1	7	2	6	6	42	51	2

June 1950 to May 1951, the bulk of the catches occurred over a six months period from August to January, inclusive. The number of hauls varied in different months and the actual numbers of larvae taken should be interpreted in the light of this variation.

From the distribution of successive developmental stages over this period it would appear that larval development requires about six months. However, such a conclusion can be only tentative. It has already been shown that in Florida the mating season may be extended for several months past the peak. Furthermore, as plankton, the larvae are carried in the direction of any currents in which they may find themselves. Under favourable conditions, larvae in the Gulf Stream may be transported for distances of over 1000 miles in a few months. It seems probable that some larvae taken in hauls in the Florida Current off Miami may not occur in their normal sequence of development. Any variation in the times of mating of populations in different areas to the south may cause the appearance of larvae of widely separated stages at the same time in the plankton farther north.

The positions at which phyllosomas of *Panulirus argus* have been taken by the "Atlantis" and by vessels of the Marine Laboratory are shown in Figure 1. In view of the fairly wide north-south distribution it is suggested that only the early larval stages of the breeding population of the east coast of Florida appear in the plankton of that area.

All the offshore specimens taken were fairly late stages, none being earlier than stage five. Except for those taken close to Bermuda, these must have drifted considerable distances from their coastal breeding grounds. It is reasonable to assume that the larvae from the Florida

population are mostly carried north in the Florida Current and that the later stages taken off Miami were probably spawned either farther south in the West Indies or else in the Gulf of Mexico.

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HYDRODYNAMICS AND RESPIRATION IN *TEREDO*[1]

C. E. LANE AND J. Q. TIERNEY
The Marine Laboratory, University of Miami

Abstract

A modification of Scholander's volumetric respirometer is described which permits the measurement of the oxygen consumption of marine organisms in an unstimulated state.

Basal oxygen consumption of *Teredo,* removed from wood, has been found to vary with size from 0.099 to 0.250 ml/hr/gm dry weight.

In place in its burrow, *Teredo* maintains a positive intramantle pressure of from 5 to 17 mm. of water. When the animals are removed from their burrows intramantle pressures vary from 2 to 5 mm. of water. Significance of these findings is discussed.

When *Teredo* is removed from wood its rate of oxygen consumption is significantly reduced.

As one phase of a continuing investigation of the energy metabolism of *Teredo,* to be reported in detail elsewhere, it became desirable to determine the rate of respiration of intact adult organisms. The conventional Warburg apparatus is inadequate for such a study because of the effects of the severe mechanical stimulation produced by the necessary agitation of the vessels. It was early found that *Teredo* when subjected to the stimulation represented by as few as 60 one cm. excursions per minute, retracted the siphons, extruded the pallets and essentially ceased to respire. Moreover, the small amount of fluid employed in the usual Warburg vessel was insufficient to provide for an adequate respiratory flow.

Accordingly, a principle first proposed by Scholander (1949) has been modified for use with small marine organisms. The surviving animal is maintained (Figure 1) in an adequate volume of aerated sea water, is not subject to mechanical stimulation, and can be observed continuously during the course of the respiration determination.

Materials and Methods

In essence the method makes use of a closed system in which the liquid and the gas phases are maintained in constant equilibrium by means of a rapidly revolving turbine partly immersed in the aqueous phase. As the animal extracts dissolved oxygen from the liquid phase

1 Contribution No. 53 from The Marine Laboratory, University of Miami. These studies were aided by a contract between the Office of Naval Research and the University of Miami in cooperation with the U. S. Navy Bureau of Yards and Docks.

in respiration, a diffusion gradient is established as a consequence of which additional oxygen diffuses into the aqueous from the gas phase. This results in a decrease in the pressure of the gas phase. Pressure changes are indicated by the compensated manometer incorporated in the system. Pressure equilibrium is restored by introducing additional air, or oxygen, from the calibrated syringe comprising part of the system. After correction for standard pressure and temperature conditions (STP), this provides a volumetric measurement of the gas consumption by the respiring animal. Since the remainder of the system is closed and maintained at constant temperature, the STP correction need be applied only to the gas present in the syringe. The second reservoir syringe (D, Figure 1) connected to the manometer

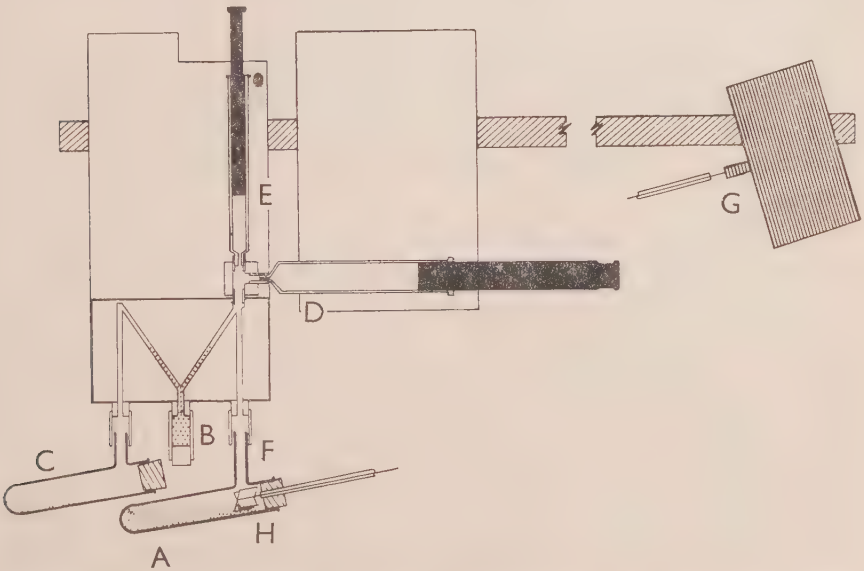

FIGURE 1. Semi-diagrammatic schema of respirometer. A, respirometer vessel; B, reservoir for manometer fluid; C, thermobarometer; D, gas reservoir syringe; E, 1 ml. tuberculin syringe, gas reservoir; F, location of carbon dioxide absorbent; G, stirrer motor to power the turbine, H.

block makes it possible either to employ larger animals with a higher respiratory rate than could be accommodated with a 1 milliliter gas supply, or to extend the observations beyond the customary hour observation period. Gas transfer from this reservoir to the main measuring syringe can be effected without significant change in the pressure

of the system because the rate of transfer can be regulated by observing the displacement of the sensitive manometer.

The plexiglass turbine comprises a cylindrical hub 20 x 6 mm. and four vanes cemented into grooves cut in the hub. The vanes measure 4 mm. x 20 mm. The grooves in which they are set are cut in a spiral fashion so as to make one complete turn in a distance of eight hub diameters. The hub is drilled longitudinally to admit the 0.016 in. stainless steel drive shaft. The dimensions of turbine, drive shaft and other elements of the assembly may be varied to suit the size of the respiration chambers employed. A rheostat-regulated laboratory stirring motor drives the turbine. The shaft is constructed of stainless steel wire of 0.016 in. diameter. This is carried in a glass shaft-log with a bore of 0.020 in. The latter is packed by blowing full of light, non-oxidizing grease after the shaft is in place.

In use the assembly is immersed up to the lower edge of the manometer block in a water bath with an observation window. The bath temperature is maintained constant at 23.5°C. plus or minus 0.01° by a combination of heating elements and cooling coils, all under precise control.

The respiration vessel (A, Figure 1) is loaded with an amount of water which will partly immerse the turbine. With vessels of different volumes the amount of water varies between 0.65 ml. and 50 ml. Filter paper, rolled into a tubular shape, is introduced into a thin-walled glass tube which fits inside the side-arm of A. This is moistened with 1 M. potassium hydroxide in amounts which vary with the total capacity of the system.

The manometer fluid reservoir (B) is charged with the proper volume of Brodie's fluid, and an adjustable screw clamp, not shown in the figure, is adjusted so that the reservoir is filled completely without air bubbles. A small amount of water is added to the thermobarometer vessel (C) in order to insure vapor saturation of both sides of the system. The volume of this water is not critical. The gas reservoir syringe (E) is attached to the manometer block through a short length of Tygon tubing. This reservoir is a 1 ml. tuberculin syringe which can be read, with a glass, to 0.001 ml. To facilitate reading the exact position of the plunger in E, the free end of the plunger is ground plane in a jig using No. 80 Garnet paper. Both the respirometer vessel and the thermobarometer are then securely stoppered, the former with a stopper enclosing the turbine shaft and shaft log and the latter an ordinary cork of good quality. The entire

assembly is then immersed in the water bath up to the base of the manometer block, the turbine is started and the system permitted to equilibrate for from 10 to 40 minutes depending on the capacity of the assembly. Then, with no further change in the set-up, the manometer fluid is elevated to the scribed marks on the manometer block with the screw clamp, and a blank determination is made. This generally is run for 30 minutes with readings being made each three minutes.

The living material is then introduced into the system with as little delay as possible, is allowed a further 10 to 30 minute period for temperature equilibration and then the respiratory run proper is begun. When *Teredo* removed from wood are used, it is necessary to add a stainless steel wire screen to the system to keep the animals out of the turbine.

The accuracy and reproducibility of the method was established

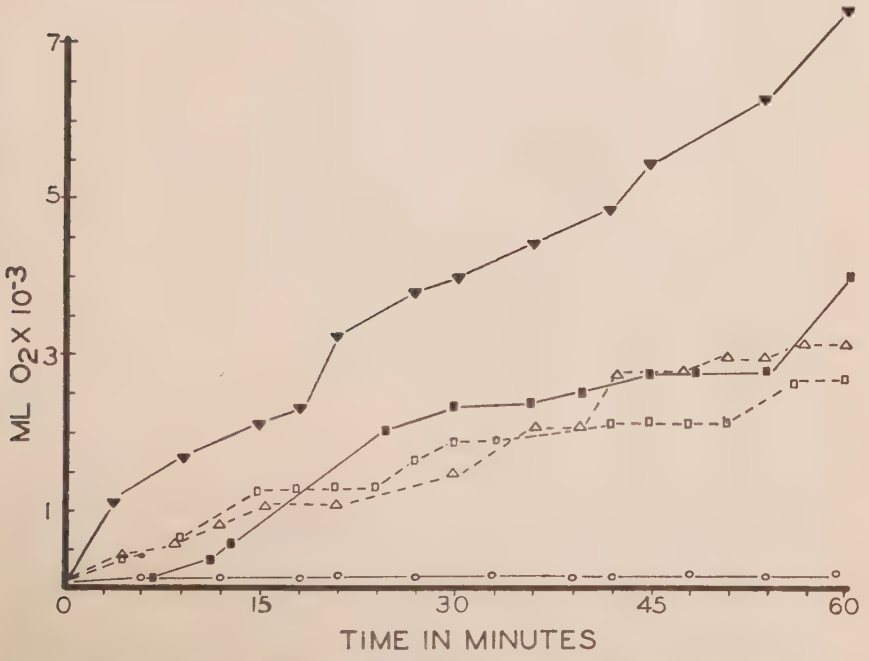

FIGURE 2. Rate and range of respiration of *Teredo* both *in situ* and after having been removed from wood. Solid lines and conventions delimit range of variation in oxygen consumption of *Teredo* in wood. Hollow conventions and broken lines delimit range of oxygen consumption for animals out of wood. Lowest line is the sea water blank.

by appropriate studies of the rate of absorption of air by degassed water, and by making an extensive series of blank runs to determine the extent of possible instrumental variations.

Animals reported in this study were *Teredo pedicellata*. These were collected by immersing standard sized collecting panels in local waters known to be infested with *Teredo* and allowing them to remain until the worms had achieved adult size.Respiration studies were conducted using both intact animals *in situ* in carefully cleaned sections of the collecting panels, and surviving adult forms which had been carefully removed from their burrows without damage to the mantle or to the siphons.

Results

Figure 2 is representative of a series of 20 similar determinations. Here are shown the ranges of oxygen consumption of animals both in and out of wood. It will be observed that the rate of oxygen uptake is not uniform but rather tends to be cyclic in nature, with maximal rates of oxygen consumption tending to recur at intervals of 10 to 15 minutes.

There is an unvarying tendency for animals within the wood to respire at a higher rate than similar forms which have been removed from their burrows. This tendency persists even though all other controllable factors, temperature, age, size, season, food and water supply, etc., be kept constant. To assist in explaining this phenomenon a preliminary study of the hydrodynamics of respiration in these animals was undertaken.

The oxygen consumption of adult *Teredo* removed from wood shows considerable variation when expressed as QO_2. An average sized worm, for example, with a dry weight of 75.3 mg. showed a QO_2 of 161.0, while a smaller adult with a dry weight of only 27.6 mg. had a QO_2 of 272.5. This inverse relationship between body weight and QO_2 was found to be generally true in all *Teredo* so far studied. It should be noted that the figures given above are for animals out of wood. Although their respiration is not normal, as will be seen later, it is reasonable to assume that the QO_2-weight relationship remains, in general, undisturbed.

Intramantle pressures were measured in animals *in situ* and out of their burrows. These measurements were accomplished by making use of a 26 gauge hypodermic needle connected by Tygon catheter tubing to a capillary manometer filled with water.

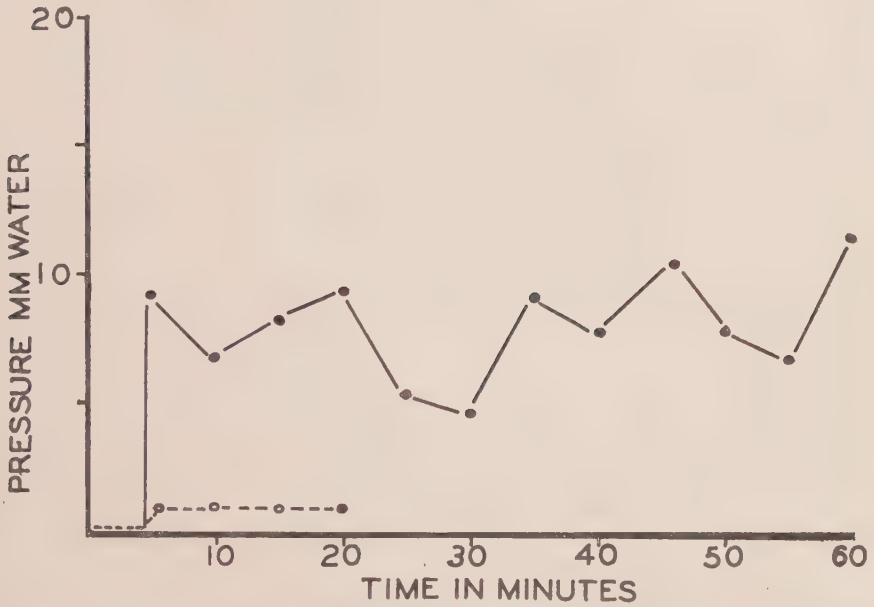

FIGURE 3. Intramantle pressure in *Teredo*. Upper line, animal *in situ;* lower line, pressure changes in another animal removed from its burrow. In both instances the needle was inserted into the mantle cavity at 4 minutes.

Teredo in situ showed a positive intramantle pressure (Figure 3) of from five to 17 millimeters of water. The average positive pressure maintained by animals out of wood was less than two millimeters of water. It will be observed that intramantle pressures of normal animals *in situ* tends to show the same cyclic variations as was noticed in the rate of oxygen uptake, but that these cycles are lacking in animals removed from wood.

DISCUSSION

The existence of a positive intramantle pressure is of fundamental significance in *Teredo*. It represents the only mechanism for maintenance of the internal turgor which is required to keep the boring end of the flaccid animal in close apposition to the head of the burrow. This was recognized by Hill and Kofoid (1927) who pointed out the importance of "turgor" in insuring that the foot and the valves remain apposed to the head of the shaft. However, they made no precise measurements of the magnitude of this force nor did they offer any explanation for its origin.

In life this positive pressure is insured by the presence of the calcareous lining of the burrow and by the presence of sphincter muscle fibers in the siphons (Posner, G. S., personal communication). These two factors interacting with the constantly-beating cilia of the gill and of the mantle are sufficient to account for the positive pressures which are repeatedly observed. When *Teredo* is evicted from its burrow one of the factors necessary to the maintenance of this positive pressure, the unyielding wall of the burrow and the calcareous lining thereof, is removed. The first consequence of this is that the volume of the respiratory stream is decreased, bringing about a necessary decrease of oxygen consumption. The other consequence is that the mantle develops herniations. The mantle itself is virtually devoid of muscle elements or of any other specific supporting elements. Thus, unsupported by shell or the wooden wall of the burrow, it is incapable of counteracting the pressure which exists within it. The result is the development of from one to several hernia-like swellings in localized areas of structural weakness of the mantle.

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SPAWNING AND SETTING OF OYSTERS IN RELATION TO SEASONAL ENVIRONMENTAL CHANGES[1]

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ABSTRACT

The environmental factors controlling spawning of oysters in the Apalachicola area were investigated with particular regard to temperature. The principal literature is reviewed. Regular observations of temperature, salinity and spatfall intensity were made at nine stations covering a distance of approximately 30 miles of Apalachicola Bay. Isolated spawning did not occur below temperatures of 22.5° C. Mass spawning took place only when the temperature rose to at least 26.0° C. On two occasions mass spawning occurred simultaneously at all stations in the eastern part of the Bay but not in the western part. The average temperature is lower in the western part than elsewhere and also fluctuates more rapidly. Since the temperature necessary for mass spawning is higher than reported elsewhere in the United States, the possibility has been suggested that there are physiological races of oysters. In the absence of observations on inheritance of this characteristic when oysters are transplanted it is considered that the interaction of a number of environmental factors upon the maturing gonad may modify the temperature reaction and that it is not necessary to postulate racial differentiation.

The environmental factors which appear to control the spawning and setting of oysters are of considerable interest to ecologists inasmuch as they undoubtedly account in part for the observed geographical distribution.

Critical temperatures for various physiological activities have been shown by Hutchins (1947) to limit the reproduction, dispersion, colonization and survival of marine animals. These critical temperatures have minimum and maximum values which establish the range of temperatures within which each vital activity can function properly. Their ranges are not necessarily the same for each vital function; hence, an animal such as an oyster may have a limited activity in an area in which the temperature ranges are such that it cannot be permanently indigenous. It may, for instance, be able to survive in a region in which it is incapable of breeding if its stock is maintained by a supply of larvae carried in from elsewhere by currents.

In the case of the oyster, the minimum temperatures for survival and

[1] Contribution No. 57 from The Marine Laboratory, University of Miami. Based on material submitted as a thesis to the Faculty of the University of Miami in partial fulfillment of the requirements for the degree of Master of Science in the Department of Zoology.

feeding are much lower than those for reproduction. It follows that larvae from a warm water population, carried into cooler waters, might develop into healthy adults even though reproduction could not occur and no permanent, self-sustaining colony would be present. Nevertheless, there is reason to suspect that some invertebrate populations are permanently maintained by this method. Different minimum critical spawning temperatures might well serve as a barrier to interbreeding of physiological sub-species of oysters and allow for a more rapid divergent evolution.

Earlier investigators held the view that *Crassostrea virginica* had one minimum critical spawning temperature throughout its range, which Gunter (1950) describes as from Canada to Campeche. This temperature was thought by T. Nelson (1928) to be 20.0°C. Earlier workers made little or no distinction between slight, sporadic spawning and mass spawning.

Various investigators have shown that slight, irregular spawnings may occur at lower temperatures than are required for a maximum or mass spawning. These aberrant, marginal cases are considered exceptional. The work of this paper is concerned with the temperatures associated with maximum spawning activity as are all references and discussions which follow. The expression "minimum mass spawning temperature" is preferred over "minimum maximum spawning temperature" due to the obvious ambiguity of the latter.

Stauber (1950) has analyzed the findings of later workers and has reported that the minimum mass spawning temperature is different in various sections of the northern part of its range (Chesapeake Bay to Canada) and suggests that, because the minimum mass spawning temperature is not the same in all areas, the existence of physiological sub-species should be considered.

Where the data permit, conclusions as to length of spawning period and minimum temperatures for mass spawning may be drawn from previous studies (Table I). In the case of the Puerto Rican oyster, spawning proceeds throughout the year and the lowest temperature of the water does not fall below 25.0°C., according to Mattox (1948). Mattox also found that spawning continued even after temperatures of 31.0°C. had been reached. It would appear from this that the maximum critical spawning temperature is higher than 31.0°C. Since this oyster is now believed to be a different species, *C. rhizophorae* (Guilding), these data are not included on the table.

It is apparent that mass spawning in *C. virginica* commences at

TABLE I.

LOWER MASS SPAWNING TEMPERATURES AND LENGTHS OF SPAWNING PERIODS*

LOCATION	LOWER MASS SPAWNING TEMP.	LENGTH OF SETTING PERIOD	SOURCE
Canada	20.0°C.	July 15-Aug. 29	Medcof (1939)
Long Island Sound	16.4°C.	July 16-Sept. 23	Loosanoff & Engle (1940)
Delaware Bay	25.0°C.	.....	Stauber (1950)
Upper Chesapeake	22-23.0°C.	June 29-Sept. 30	Engle (1950)
Eastern Bay Chesapeake	25.0°C.	June 29-Sept. 30	Engle (1950)
South Carolina	.....	End of May-Nov.	Higgins (1928)
Texas	25.0°C.	May 15-Sept.(?)	Hopkins (1931)

* Small deviations must be expected.

different temperatures at different locations within its range. In general, these critical temperatures appear to be higher where the average temperature of the local waters is higher. It is also to be noted that the spawning season is longer in the southern and warmer waters.

It is logical to suppose that Canadian waters might be cooler and that the mass spawning temperatures might be the same or lower and the spawning season shorter than in the waters of Long Island Sound. Nevertheless, the critical spawning temperature for the oyster in Canada is higher than that of Long Island Sound. This apparent discrepancy was resolved by Stauber (1950) when he showed that the temperatures of Bideford River in Canada, where the observations on critical spawning temperatures were taken are actually higher on the average than those of Long Island Sound during the months from June to August.

Loosanoff and Engle (1940) found that the intensity of oyster set was largely independent of the fullness of the gonads. They were unable to find a direct correlation between water temperature before spawning and thickness of the gonadal layers.

The findings of Prytherch are in contradiction to those of Loosanoff and Engle but appear to be exceptional. Prytherch noted that in Milford Harbor, not far from Long Island Sound where Loosanoff and Engle worked, there was a direct correlation between temperature, thickness of gonads, and intensity of spat-fall.

The spawning reaction of oysters was found by Galtsoff (1930, 1934, 1938a, 1938b, 1940) to be the result of a complex of interacting agencies. He found that temperature alone was largely unsuccessful in inducing spawning. However, he noted that spawning could be provoked by the addition of a small amount of sperm to the water. The

spawning reaction was apparently specific, because no positive response was obtained when the sperm of *Mytilus* or *Mya* was used. The spawning reaction was followed by a refractory period during which the organism was insusceptible to sperm. In *C. virginica* this period lasted from two to five days.

Males were found to respond to the addition of eggs almost immediately by releasing sperm. The active principle of the eggs, unlike that of the sperm, was observed to be soluble in sea water. Males not only responded to eggs but to sperm as well.

Galtsoff (1930b) concluded that males respond more readily than the females to the increase in temperature and, under natural conditions, are apparently the first to spawn. The reaction, once started by one of the males, stimulates the females and males nearby, which in turn stimulate the others. In this way mass spawning is achieved. The chemical stimulation is influenced in two ways by the temperature. The latter determines a lower limit below which the females fail to spawn, and also supplies the initial stimulus for spawning of the males.

Various others have reported that the length of larval life increases at low temperatures. Medcof (1939) states that at temperatures varying from 19°C. to 21°C., the length of larval life of Canadian oysters varies from 30 to 24 days respectively. Prytherch (1928) observed a larval period of from 13 to 16 days at slightly higher temperatures (21.3°C. to 23.2°C.). Loosanoff and Davis (1950) have found that larval development and setting, as well as spawning, may occur at temperatures lower than those accepted as the critical minimum, provided that egg and sperm suspensions are present. These workers and Thorson (1946) suggest that oysters and other marine invertebrates may have two minimum critical temperatures associated with reproduction. The temperature required for the maturation of sexual products may be lower than that required for spawning.

Butler (1949) found that gametogenesis was inhibited in oysters kept in brackish water for long periods. A return to the level of gonad activity characteristic of oysters kept under normal conditions of salinity only took place several months after return to water of higher salinity. Butler attributed the marked variation and suppression of gonad activity to variations in food availability rather than to the direct action of low salinity in the surrounding water. Hopkins (1931) also shows that larval development is retarded by low salinity, apparently as a result of its effects upon the food supply. He suggests that

salinities above 6 parts per thousand are necessary for complete development.

In view of the lack of any published data on spawning and setting in Florida waters, which are warmer for longer periods than those of the Atlantic oyster grounds, the opportunity was taken to observe the periods of spawning and setting, together with the physical conditions of the sea water in Apalachicola Bay, Florida during 1949 and 1950. This was carried out as part of a survey primarily intended for the determination of the proper times and places for planting cultch in a program for restoring unproductive oyster beds to their former usefulness. The author is grateful to Dr. F. G. Walton Smith, Director of the Florida State Oyster Division and of the Marine Laboratory, University of Miami for his continual guidance and inspiration and to Mr. Charles Dawson and Miss Sandra Benson who made many of the routine observations. The cooperation of Mr. George Vathis, Supervisor of the Florida State Board of Conservation, is also gratefully acknowledged.

Description of the Region

The area investigated includes St. George Sound, Apalachicola Bay, and St. Vincent Sound, as well as Indian Pass Lagoon (Figure 1). In

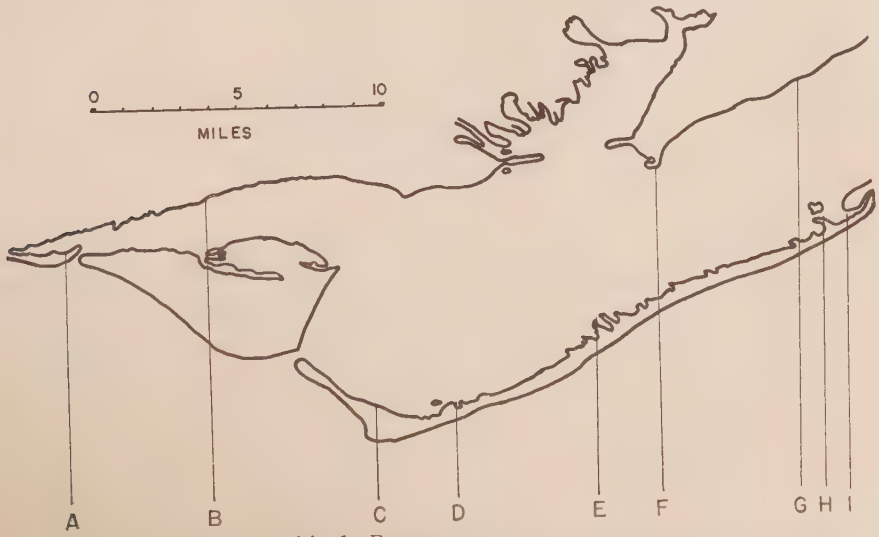

Figure 1. Map of Apalachicola Bay.
A, Indian Pass; B, Thirteen Mile; C, Government Dock; D. Pilot's Cove; E, Nick's Hole; F, Cat Point; G, Porter's Bar; H, Goose Island; I, East Slough.

length, it extends from 84° 40′ to 85° 15′ 30″ West Longitude. It is approximately 36 miles long. The width of Apalachicola Bay varies from about 14 miles to one mile with the average being about five miles. Having an area of approximately 180 square miles, and being protected by the outlying St. George and St. Vincent Islands, it constitutes one of the most favorable spots in Florida for the commercial production of oysters.

The Apalachicola River enters at about the center of the Bay and is formed at the confluence of the Flint and Chattahoochee Rivers near Chattahoochee, Florida, approximately 107 miles north of Apalachicola Bay. Both of the streams that form the Apalachicola River carry a great burden of red silt which is eventually deposited in Apalachicola Bay, constituting a great problem from the standpoint of oyster cultivation.

In typical delta fashion, the Apalachicola River divides several times at the mouth forming many short, shallow and sluggish secondary streams, all of which constitute the mouth of the river. The more important of these are the Apalachicola River, the St. Marks River, and the East River. Adjacent to the mouth of East River to the east, another independent stream, Whiskey George Creek, enters in the Bay. Together, these streams furnish almost the entire fresh water supply for the Bay.

The extreme shallowness of the Bay is one of its most outstanding features. The average depth of water is approximately five feet. The maximum recorded depth is a small pass between oyster reefs which is 32 feet deep. Shallow flats abound which at low tide have only inches of water.

Direction and intensity of winds are extremely important factors in determining the types of habitats to be found in Apalachicola Bay. The prevailing winds are from the east and there is a consequent drift of high salinity water from East Pass through Apalachicola Bay. In the region of the multiple mouths of the Apalachicola River this salty water is diluted and drifts westward through St. Vincent's Sound and out into the Gulf of Mexico through Indian Pass.

There are many temporary modifications of these conditions. A north wind which blows steadily for several days with strong force may blow a great deal of the water out of the Bay. This results in lowered salinity as the river water spreads out unimpeded over the bottom. Conversely, a strong wind from the south for several days can bring dangerously high tides and a high salinity.

Oyster reefs and "lumps" are found scattered in abundance from the Goose Island region of St. George Island westward throughout the Bay. With the exception of salinity differences the bars represent ecologically similar habitats.

With the exception of the oyster reefs and bars which are made of tightly packed shell of ancient origin and which stand boldly in relief, the bottom of Apalachicola Bay is extremely soft. The light, fine particles of red silt have formed a temporary sediment over the entire area. Any disturbance of the water raises this at once, after which, when the waters again become calm, it is redeposited.

Indian Pass Lagoon Station is situated on the south shore of Indian Pass Lagoon approximately one mile west of West Pass. The baskets of shell were maintained about 10 yards from shore in two feet of water, low water springs. The bottom is extremely soft, having only a small component of sand. Despite this fact, numerous single and clumped oysters are scattered over the bottom sparsely. Producing bars abound in the Lagoon although most of them are exposed at low water.

Thirteen Mile Station was maintained 13 miles west of the mouth of the Apalachicola River on the north shore of St. Vincent Sound. The shell baskets were hung from a dock at a depth of one foot, low water springs. The bottom is composed of shell debris, much silt and small amount of sand. "Coon" oyster bars are abundant. The general region is shallow, being about two or three feet deep at low water springs.

Government Dock Station was established at the end of the light house dock which extends northward into Apalachicola Bay from St. George Island. Depth of water at this station is about 15 feet at low water springs. The baskets of shell used to collect spat were suspended from the dock by a wire at a depth of three feet, low water springs. There are no oyster bars of any type in this general area. The southernmost end of St. Vincent's Bar, in area the largest bar in the Bay, extends to within half a mile of Government Dock. The bottom is very hard and is composed of closely packed sand.

Pilot's Cove Station was installed on the east side of the mouth of Pilot's Cove on St. George Island. Pilot's Cove is a shallow tidal bay of irregular outline. Most of the bottom, which is a mixture of sand and soft mud, emerges at low water springs. "Coon" oyster bars are scattered over the entire area. In the few places that the oysters are not exposed at low water, they are of marketable size and flavor.

Nick's Hole Station is located on the east side of the mouth of Nick's Hole. This bay extends into St. George Island for about a quarter of a

mile. The depth is shallow, never exceeding five feet at low tide, and becomes gradually more shoal as the southernmost extremity is reached. In its upper reaches the water is only a few inches deep at neap tide. In this area non-commercial oyster bars abound which support oysters of low quality. This is due probably to emergence from the water at low tide. There are also a few small areas of producing oyster beds in the vicinity.

Cat Point Station is similar in many respects to the Porter's Bar Station and is adjacent to one of the most productive oyster bars in the Bay. It was established at the northernmost extremity of Cat Point which, like Porter's Bar, touches the north shore of St. George Sound. The Cat Point spat-fall checking point is nearer than Porter's Bar to the Apalachicola River. The baskets of shell used to collect spat were kept about 10 feet from shore. The water depth here at low water springs is about one foot. The bottom is composed of sand, shell debris, and silt.

Porter's Bar Station was placed on the north shore of St. George Sound. Porter's Bar, which extends about three quarters of the distance across the sound at this point, has its northernmost extremity contiguous with the beach. The station was maintained about 50 feet from shore in about two feet of water, low water springs. The bottom is a mixture of sand and fine silt.

Goose Island Station was established centrally on the eastern side of a slight peninsula jutting northward from St. George Island into St. George Sound. This peninsula would be contiguous with Goose Island except for the narrow gap which lies between the two areas. Many "coon" oyster bars lie in the immediate vicinity.

East Slough Station is located in the center of a long, narrow bay at the eastern end of St. George Island, east of, and adjacent to, Goose Island. Within the memory of people now living in Apalachicola this area of the Bay has never supported commercial oyster production. The mouth is approximately 100 yards wide. The width gradually tapers towards the east until at its extremity, about a quarter of a mile from the mouth, it is not more than 15 yards in width. Numerous "coon" oyster bars are found at the mouth of East Slough, and in the vicinity of Goose Island, although none are found in the shallow waters of the Slough. They stand out of water at low tide.

Methods

Preliminary temperature observations and studies of gonad condition were begun in Apalachicola Bay, Florida, on February 10, 1949,

and were continued until February 16, 1949. Gonads were again examined on February 20, 1949, and from that date, at intervals of approximately two weeks, throughout the summer and fall.

An attempt was made during the winter of 1949 and spring of 1950 to make a complete survey of all existing oyster reefs in Apalachicola Bay, and to evaluate the condition of oysters found in each locality. Glycogen analyses were carried out according to the method of Hagendorn-Jensen (1923). Condition index was determined by the method of A. E. Hopkins and described by Higgins (1938).

Both glycogen analyses and condition index studies were made on aliquots of ground oyster meats from every sample investigated.

Abundance of larvae in the plankton was not used as an indication of mass spawning, since various workers in the past have found poor correlations between larval concentrations and spawning intensity (Prytherch, 1928; Galtsoff, 1930; and Loosanoff and Engle, 1940). Identification of mass spawnings by weekly gonad examination of large numbers of oysters was not a practical possibility during the present study.

Different workers have reported various findings relative to the migration of oyster larvae. Prytherch (1928) concluded that most of the set is found within 300 yards of the place of spawning. More recently Carriker (1951) found that the younger stages move passively with the ebb and flow of tide, but that older stages tend to drop to the bottom on the ebb and to rise on the flood. Thurloe Nelson and his associates have shown that in Barnegat Bay, oyster larvae may be distributed over several miles by water currents. In view of the tidal nature of currents at Apalachicola and in view of the considerable area over which the stations are scattered, it is believed that the spatfall at each station provides a reasonably satisfactory index of spawning in the neighborhood of that station. The number of larvae carried over the rather large distances between stations is not believed sufficient to account for mass settings.

Spat-fall was observed by means of baskets, made of chicken wire, containing 150 to 200 well-bleached oyster shells of consistent size. The baskets were tightly packed to prevent movement of shell and consequent loss through the mesh.

The spat-fall study was begun on March 23, 1949, when wire baskets filled with shell were first placed in the water at four of the stations, Indian Pass Lagoon, at the western-most end of Apalachicola

Bay; Thirteen Mile, 13 miles west on the mainland from the town of Apalachicola; Cat Point, which juts into Apalachicola Bay on the eastern side of the mouth of the Apalachicola River; and Porter's Bar, about six miles east on the mainland from the River mouth. Nick's Hole, and Pilot's Cove, were established on April 6. On May 11, the last two stations were started. These were Goose Island and East Slough. The last two stations were checked every two weeks until December 30, 1949. Porter's Bar was maintained until December 16, and Thirteen Mile which was last checked on December 4, 1949. Although vagaries of the weather sometimes prevented the checking of stations on appointed days, these occasions were infrequent.

At the time of each station visit, temperature was recorded, density of the water was observed, and the exposed basket of shells was brought to the laboratory after being replaced by a new basket. The intensity of setting was determined by counting the spat on the inside of 20 shells from each basket. In order that the younger, more minute spat could be found and counted, a binocular dissecting microscope was always used for shell examinations. Notes were also made with reference to other fouling organisms likely to compete with oysters for substrate, and observations were made as to relative silting of shells. Number of spat on 20 shells is used as a unit throughout this study.

Temperatures were always taken at the surface. As Apalachicola Bay is extremely shallow, and the waters in it are constantly mixing, the bottom temperatures are usually within a half a degree of those at the top. Several correlative temperatures taken simultaneously at the surface and at three foot depths were found to be approximately the same, with the maximum variation being half a degree Centigrade.

Inasmuch as salinity changes may possibly act not only directly upon oyster reproduction by affecting the tissues, but also indirectly by their influence upon feeding and nourishment, measurements of salinity variations were carried out simultaneously with temperature measurements.

General observations on the presence of silt, predators, and of organisms which compete for space on the collecting shells were made at all stations.

Observations

Gonad Development. Temperatures sufficient to induce mass spawning of oysters in Long Island Sound and Canada were present in the waters of Apalachicola Bay by the 12th of February, 1949. At that time, however, the gonads were only faintly visible.

On February 20th a survey of all stations in the Bay was again made to determine the state of development of the oyster gonads. They were found in almost every case to be well-convoluted, and in a thickened condition. Microscopic examination of sex products was made and they appeared to be mature. Ova were well-formed and sperm were active.

Gonad examination was continued at intervals of about two weeks until the first week in August, when a high percentage of oysters from all habitats checked showed mature gonads. There were usually a number of oysters in each area that had released their sex products. The relative numbers of spawned and unspawned individuals varied with the habitat and the time of checking. There appeared to be no mass release of spawn by the entire population, such as characterizes of the oysters of Canada and Long Island Sound.

After the first week of August there was a marked increase of spawned individuals in all habitats. This trend continued until the last week of August when it was difficult to find any oyster with ripe gonads. A survey during the second week of September failed to reveal a single oyster filled with spawn. That such individuals were present in some numbers is attested to by the late set of spat which occurred in several parts of the bay. Apparently the survival rate of larvae is high, as a relatively few oysters have produced much of the spat which set during September, October, and November.

SALINITY. Salinity readings are summarized in Table II. The least fluctuation of salinity, measured in terms of standard deviation over an 18 month period, was at Indian Pass, and Porter's Bar. The greatest fluctuation was at Government Dock and St. Vincent's. Over weekly periods, Indian Pass showed least fluctuation and St. Vincent's the greatest. Over tidal periods the least fluctuation occurred at Porter's Bar and the greatest at Nick's Hole and St. Vincent's. The lowest recorded salinities were at Nick's Hole. The highest occurred at Indian Pass. Low salinities in general were associated with large fluctuation.

The extremely rapid and frequent salinity changes cited here were previously reported by Ingle and Dawson (1950).

TEMPERATURE AND SPAWNING. The weekly temperature readings are summarized in the accompanying diagrams, upon which are also plotted the observations of spat-fall. Temperatures during February are shown in Table III.

Indian Pass Lagoon. Assuming that, at the temperatures encountered, the larval stages of *C. virginica* last about fifteen days, as shown by

TABLE II

SUMMARY OF SALINITY OBSERVATIONS TAKEN DAILY, WEEKLY AND TIDALLY. COMPARED WITH PRODUCTION ESTIMATE AND MAXIMUM OBSERVED GLYCOGEN CONTENT.

	18 *Months*			*Weekly*		*Tidally*			
Station	No. of Samples	Range	Standard Deviation	Average Range	Greatest Range	Average Range	Greatest Range	Average Range	Production	Glycogen % wet wt.
Porter's Bar	158	0.0 to 42.5	6.1	19.8	15.4 to 42.5	7.7	9.2 to 13.1	1.9	Heavy	1.3
Indian Pass	143	16.1 to 43.8	6.1	27.2	10.7 to 35.0	5.9	25.0 to 33.3	3.1	Heavy	5.6
Cat Point	144	0.0 to 32.1	6.2	15.6	0.0 to 22.2	7.1	8.0 to 23.0	4.8	Medium	0.4
Goose Island	33	7.0 to 32.7	6.5	20.6	10.7 to 26.0	4.7	. . .	. .	None	. .
Pilot's Cove	68	11.9 to 42.4	7.0	25.5	20.5 to 35.6	8.3	. . .	. .	Small	0.3
East Slough	28	5.9 to 32.9	7.1	21.6	11.4 to 24.2	4.8	. . .	. .	None	. .
Nick's Hole	83	0.0 to 33.6	7.3	17.5	0.0 to 20.3	7.4	7.2 to 15.6	6.9	Small	1.7
Govt. Dock	49	4.8 to 42.8	7.4	22.2	16.7 to 42.8	9.2	. . .	. .	None	. .
St. Vincent's	197	2.6 to 34.9	8.3	22.1	10.8 to 34.0	12.0	14.1 to 30.2	6.6	None	0.9
Miller's (13)	113	3.3 to 43.8	9.4	20.6	3.5 to 33.7	10.2	5.0 to 22.7	6.7	None	0.7

1. Salinity in parts per thousand. Period of sampling, February 1949 to July 1950.

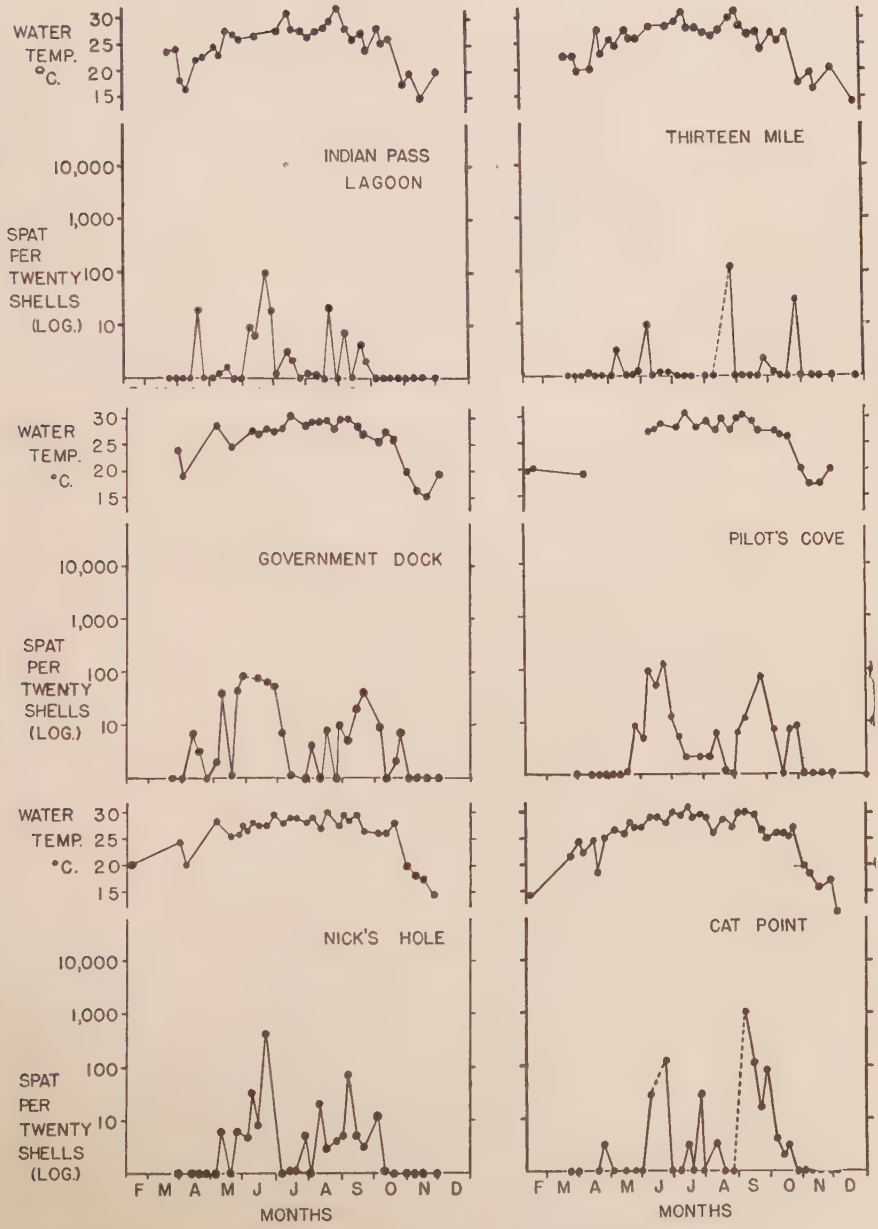

FIGURE 2. Relation of spatfall intensity to temperature changes.

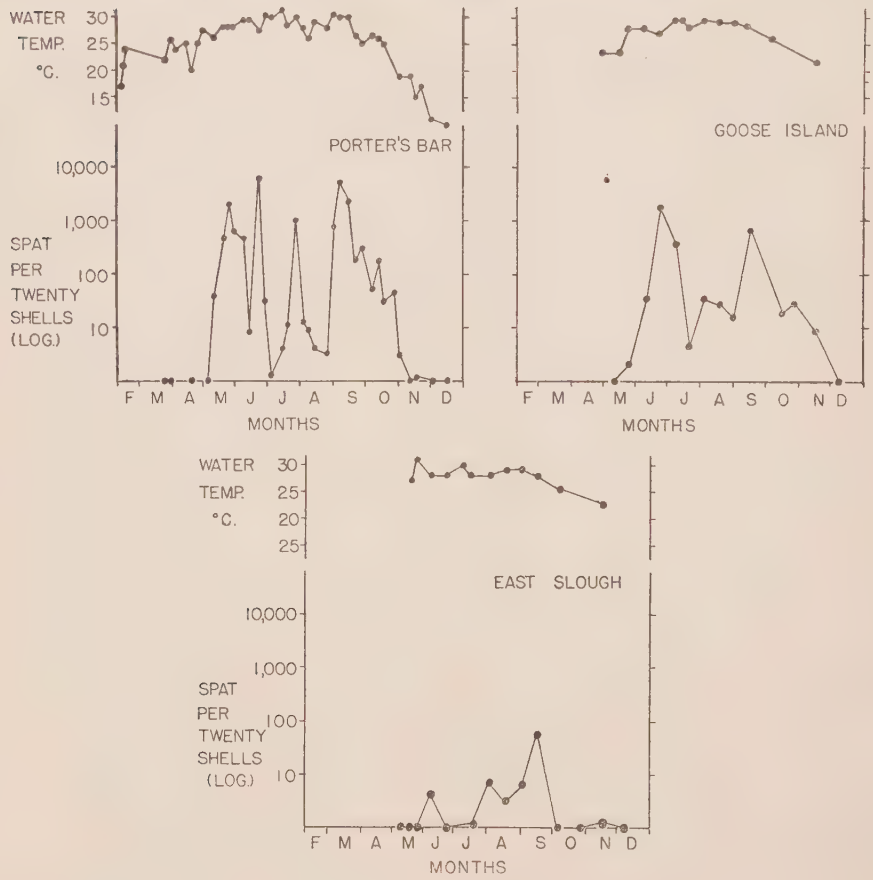

FIGURE 3. Relation of spatfall intensity to temperature changes.

previous workers, the first isolated setting, which occurred during the third week in April, must have been spawned not earlier than the first week in April. The release of sex products did not occur, therefore, until the temperature of the water had reached at least 23.0°C. in two successive weeks. The cooler temperature of the water at certain times during the two weeks before may have delayed setting.

Temperatures of above 25°C. existed during several weeks before the first mass spawning which occurred during the second week of June. Previous to this spawning peak, the lowest recorded temperature for three weeks was 26° C.

A small spawning maximum apparently occurred about August 10

TABLE III

TEMPERATURE OBSERVATIONS IN APALACHICOLA BAY DURING FEBRUARY 10-16, 1949.

LOCATION	2-10	2-11	2-12	2-13	2-14	2-15	2-16
St. Vincent's Reef	14.5	. . .	16.8	. . .	. . .	18.0	. . .
South of Bridge	. . .	13.5	. . .	. . .	. . .	. . .	. . .
Paradise Flat	. . .	. . .	. . .	. . .	19.0	. . .	. . .
Sand Island Flat	. . .	. . .	. . .	. . .	. . .	19.0	. . .
East Hole	. . .	14.5	. . .	. . .	. . .	. . .	. . .
Hagen's Flat	. . .	. . .	14.5	. . .	. . .	. . .	. . .
Nick's Hole	. . .	. . .	. . .	. . .	. . .	. . .	20.5
Thirteen Mile	. . .	. . .	. . .	. . .	19.0	. . .	. . .
Porter's Bar	. . .	17.0	21.0	24.0 & 20.0	. . .	. . .	. . .
Pilot's Cove	. . .	. . .	. . .	. . .	. . .	19.7	. . .
Cat Point	. . .	14.0	. . .	. . .	. . .	. . .	. . .
Cat Point (s)	. . .	14.0	. . .	. . .	. . .	. . .	. . .
Cabbage Lump	. . .	. . .	16.8	. . .	. . .	. . .	. . .
Big Bayou	. . .	. . .	. . .	. . .	20.0	. . .	. . .

when the water temperature was 27.5° C. For seven weeks prior to this spawning the temperature observations averaged 28.2° C.

Between September 21, and September 28, the temperature dropped from 27.0° C. to 24.0° C.

Thirteen Mile Station. Since collecting baskets at this station are in fair position to receive an occasional spat from other areas, the rather meager set that occurred during the early part of the season may have been derived from premature spawnings that occurred not only in the vicinity of the station but also in other parts of St. Vincent Sound. The set of April 14th consisted of one per 20 shells only. That of May 11th numbered three spat per 20 shells. Both of these were preceded by temperature of over 22.5°C. at the probable spawning date. The only significant maximum was during the week ending August 25, when 118 spat fell per 20 shells. The lowest observed temperature for seven weeks prior to the probable date of this spawning was 26.5°C., while the average of the weekly temperature readings for this period was 28.9°C.

Government Dock Station. The first detected spat of the season fell at Thirteen Mile Station and at Government Dock. In both cases the attachment was made during the week ending April 14th. It is therefore fairly certain that the first slight spawning occurred about March 30th, when the temperature of the water was observed to be 24.0°C.

Spat-fall at Government Dock Station in all probability originated as spawn from St. Vincent's Reef. There are no oysters in the immedi-

ate vicinity of Government Dock. The nearest are some distance away at St. Vincent.

The temperatures at Government Dock therefore have little bearing on the production and release of spawn and only give an indication of temperatures at which larvae will set.

Pilot's Cove. An initial slight spat-fall took place on May 18. The temperature of spawning was not recorded. A temperature of 28.5°C. was attained by the sixth of June after which it was not observed to fall below 27.5°C. A temperature of 27.5-28.5°C. prevailed about the time of spawning for the heavy set of June 22nd. There was apparently no production of spat sufficient for detection after temperatures dropped below 26°C.

Nick's Hole. A minor degree of spawning apparently occurred during the last week of April and resulted in observed spat-fall of the week ending May 11th. Unfortunately no temperature was recorded between 28°C. for May 5th and 20°C. for April 11th.

Mass spat-fall was observed during the week ending June 22nd. Spawning which produced this group presumably took place about June 8th when the recorded water temperature was 28°C.

Other maxima of spat-fall, minor in nature, occurred for the weeks ending August 10th, and September 7th. Spawning for the former would have taken place between July 20th and July 28th when the recorded temperatures were 29.0°C. and 28.0°C. respectively.

Spawning that produced the September maximum presumably took place between August 19th when a water temperature of 30.0°C. was observed, and August 26 when 27.5°C. was recorded.

Although no peak occurred subsequent to September there was almost no break in spawning activities during the remainder of the season until October 12th. During this period of relatively unbroken reproduction the lowest recorded water temperature was 26.0°C. The water temperature dropped after October 20th when it was 28.0°C. No spat was recorded subsequent to this.

Cat Point Station. The spat-fall at Cat Point was less than might be expected, although, physically, its location was similar to that of Porter's Bar Station.

Although wave action is strong here, it cannot be responsible for the mediocre set. Porter's Bar Station experienced at least as intensive action by waves and yet produced the greatest amount of spat of all stations.

The first observed isolated set was on June 8th. The temperature at the probable time of spawning was 27° C. During the previous two weeks the temperature was maintained above 26.0°C.

The first maximum of set appeared during the week ending September 7th. Spawning presumably took place between August 18th and August 25th when water temperatures were 28.5°C. and 27.0°C., respectively.

The temperature began to descend during the latter part of September, and there is no evidence that larvae were produced after October 6th when the temperature was 26.0°C.

Porter's Bar Station. The most extensive data for the study of spawning was obtained here. The spat-fall was heaviest, the maxima most pronounced and more numerous. The likelihood of spat from other localities confusing the results was at a minimum, due to the fact that the movement of water in Apalachicola Bay is predominately from east to west. As there are at present no oyster bars to the east of Porter's Bar, the likelihood of larvae being carried to this station from other areas was negligible.

The onset of spawning apparently occurred about April 27. This is established by the fact that 37 spat fell on 20 shells during the week ending May 11. Prior to the time of spawning, no temperature was recorded which exceeded 25.5°C. The first maximum of spawning occurred during the week ending May 25, indicating that mass discharge of sex products took place about May 4th when the temperature was 27.5°C.

The second maximum of set, during the week ending June 22, was the greatest recorded for any station of Apalachicola Bay for any period during the summer of 1949. The temperature recorded for the probable time of spawning was 29.5°C.

Spawning was continuous until the next maximum which occurred during the week ending July 28th. The spawning temperature on July 14th was again 29.5°C.

The fourth principal setting period took place during the week ending September 7th. The spawning date was about August 25th at which time the water temperature was 28.0°C.

On October 19th, a water temperature of 25.0°C. was recorded after which the temperature continued to fall, reaching 19.0°C. on November 3rd. There was a negligible amount of spawning after October 13th, when the temperature was 26.0°C.

Goose Island Station. The first recorded set was on May 25th. At the time of spawning temperatures were near 23.5°C.

The first heavy set of spat occurred during the week ending June 22nd when 1752 spat were counted on 20 shells. The spawning which was responsible for this spat-fall presumably took place about June 8th. The observed temperature at the time of spawning was 28.0°C.

East Slough Station. Spat apparently did not get into the upper reaches of East Slough in any substantial amounts, despite the fact that at the mouth, not over a quarter of a mile away, numerous coon bars are found. It appears that oyster larvae are poor swimmers horizontally in this area. There is not a strong movement of water along the axis of East Slough in its more distal parts, and the relatively poor ability of the oyster larvae to negotiate a distance of perhaps one eighth of a mile unaided by currents probably explains the poor set in East Slough. This conclusion is further strengthened by the fact that an excellent set of spat occurred at Goose Island, in the vicinity of, and ecologically similar to, East Slough except for the presence of horizontal water currents.

The first small set at East Slough was on June 8th. Temperatures at the time of spawning were already 27° C.

Competitors for Substrate Space. In Apalachicola Bay the most serious competitor for attachment space is the barnacle, *Balanus improvisus* Darwin. This fouling organism was found in abundance during the entire period of the spat-fall study (February to December, 1949). For this reason, shell planted in Apalachicola Bay may be presumed to have lost almost all of its efficiency as oyster cultch after a period of one month. In that length of time it is estimated that usually the entire surface of each shell will be covered by barnacles, thus preventing the set of oyster spat.

Next in importance to the barnacles as a competitor for substrate space was the limpet, *Crepidula fornicata* (Linneaus). While in most cases the number of *Crepidula* which colonized experimental shell was not great, a rapid growth made them pests. It was found that the accelerated growth of the oyster spat during the first five weeks of post-larval life was equalled approximately by that of the limpet. In the case of both animals this growth was found to be approximately one inch under favorable circumstances. However, the oyster maintained its growth rate whereas the limpet grew very little after it reached one inch. The largest *Crepidula* observed measured only one and three-sixteenths inches.

Two other organisms utilize space which might otherwise be available to oysters. *Mytilus recurvus* Rafinesque, (syn. *Mytilus hamatus* Say), is the least noxious of these and probably, alone, would not ever be a serious menace to setting spat. However, its tendency to grow in clusters sometimes results in young oysters being surrounded and covered.

Schizoporella unicornis (Johnston), a bryozoan, grows with extreme rapidity. Unimpeded, a colony of this organism could probably cover an oyster shell in about three weeks. Fortunately, it seems to thrive mostly on the under sides of shells and, in the case of the experimental baskets, was found predominantly on the shells located near the center. For this reason there was little apparent competition between *Schizoporella unicornis* and oyster spat as the latter preferred unsheltered substrate.

Silting. Under conditions existing during this study, silting was not considered to be of critical importance.

On extremely rare occasions, a deposit of millimeter thickness was observed. In these cases no spat-fall was observed, possibly due to the mechanical difficulty involved in making attachment.

Condition. During the winter of 1949-50, 81 samples were checked for condition. The index was found to vary from 2.4 to 13.9, and the average of all samples was 6.0. This rather low average is an indication of the watery nature of Apalachicola oysters in general and is supported by the low glycogen findings reported below.

Glycogen Determinations. The highest recorded glycogen content was in oysters from Indian Pass (Table II). The poorest oysters in this respect came from Pilot's Cove, Cat Point and St. Vincent's Reefs. In general, the oysters of Apalachicola Bay are of relatively low glycogen content and poor condition index. Aside from one instance, when a content of 5.6% wet weight was reported for Indian Pass Lagoon, the samples analysed all contained less than 1.7% glycogen, wet weight.

Discussion

The spawning of oysters began, in isolated cases, during the last week in March when the water temperature was 22.5 °C. in nearby waters (Thirteen Mile).

There may have been even earlier spawnings, not numerous enough to be detected on the spat-fall stations. As previous workers have shown, critical temperatures are better defined and more reliable in the case of mass spawnings than in isolated cases.

Although an exact critical temperature for mass spawning may not exist in Apalachicola Bay, and would be difficult to determine under any circumstances, it is possible to make certain statements as to minimal requirements.

It is noted that in no case did mass spawning occur at a temperature less than 26.0°C. The mass spawning listed for October 26th at Thirteen Mile has a doubtful status. Moreover, in each case of mass spawning water temperatures were consistently above 25.0°C. for several weeks prior to the release of sex products. The first mass spawning was recorded at Porter's Bar during the week ending May 11th.

The most striking fact presented in Figures 2 and 3 is the simultaneous mass spawning in various parts of eastern Apalachicola Bay during the first week of June. The oysters of five regions, Goose Island, Pilot's Cove, Nick's Hole, Porter's Bar, and Cat Point, apparently released their spawn at that time when the average temperature for all of these stations was 28.4°C. A second simultaneous peak at these stations occurred in September.

Other spawning peaks, which occur simultaneously in habitats of the same general region, may be noted throughout the summer. The lowest temperature recorded for any of these spawnings was 26.0°C.

The peaks of spawning intensity were found to exist against a background of more or less continuous spawning at most of the stations.

Naturally, in any process as complicated as spawning, there will be a few individuals that will be slower or which, for some reason, fail to exhibit a completely normal response. These few individuals could account for the almost continuous spat-fall between peaks.

Multiple spawnings are reported from other areas of the United States and Canada and more than one peak of reproductive activity in the course of one spawning season is considered normal. To that extent, and from the standpoint of intensity, Porter's Bar apparently enjoys the finest environmental conditions from the standpoint of spawning. A total of four spawning peaks was recorded for one season, all of which were heavy.

Spawning in the eastern part of the Bay was much stronger than that in the western sectors. Thirteen Mile and Indian Pass Lagoon each had only one definite peak of spawning, which occurred during the week ending August 10th. At all times, even during the most intensive periods, spat-fall at both of these stations was light.

These stations did not participate in the simultaneous spawning of other stations during early June and September. The reason for this

is not clear. It is possible that temperature changes were sufficiently uniform over the eastern stations for oysters to react similarly at similar times. At Indian Pass Lagoon and at Thirteen Mile the temperature was lower on the average and showed a definitely greater amount of fluctuation than elsewhere. At these two stations the salinity was higher and fluctuated less than at the remaining stations. It may be possible that this could be responsible for reducing the intensity of spawning. It is worth noting that, in spite of poor spawning, the oysters in this part of the estuary are of better quality and give a higher yield to the oysterman than elsewhere.

As Table II shows, all parts of the Apalachicola Bay are exposed to the extraordinary rigors of a rapidly varying salinity, and the low glycogen content of indigenuous oysters may be due, in part at least, to these unstable environmental conditions. These oysters of low vigor nevertheless produced prodigal amounts of oyster spat.

The data indicate that a higher minimum critical temperature for mass spawning exists in Apalachicola Bay than is found anywhere else in the United States. While keeping in mind the possible existence of physiological races, it is prudent also to remember that local environmental conditions may have the effect of making the spawning act more sluggish. The existence of physiological races cannot, in any case, be demonstrated until the characteristics have been shown to be inherited.

As an illustration, the minimum winter water temperatures of Long Island Sound, Chesapeake Bay, and Delaware Bay are substantially below those found in Apalachicola. The monthly winter averages of the first three locations would also be less than those of the latter. It is possible that the lower winter temperatures could "condition" oysters to spawn at a lower temperature.

Distinct care should be taken not to ascribe spawning reactions entirely to temperature. Conditions which determine the time of ripening of the gonad may be of greater importance than the stimulus which initiates spawning. If gametogenesis proceeds slowly during a time of rapid rise of water temperature, mature gametes may not be ready for release until relatively high temperature is reached. This delayed action resulting in an apparently high minimum mass spawning temperature was noted by Medcoff (1939).

In the case of Apalachicola oysters, where a rigorous hydrographic environment apparently results in a relatively poor oyster, the lack of glycogen may be responsible for a depressed gametogenesis. Butler's

conclusions that low salinity retards gametogenesis indirectly by affecting nourishment supports this view.

Silting, during usual conditions, was not found to interfere with spat-fall. Although there is normally a rather rapid deposition of silt in Apalachicola Bay, the oysters were able to penetrate to the substrate and settle. Over a period of several weeks the overlay of silt plus microscopic organisms increase until some interference is noted. Under conditions where cultch planting is well-integrated to the spawning cycle, however, silting can be eliminated as a deterrent to setting.

Barnacles (*Balanus improvisus* Darwin) are serious competitors for substrate space during the entire year. When optimum conditions for barnacle setting and growth are present, fresh cultch loses almost all of its usefulness for oyster attachment after about four weeks. *Crepidula* and *Mytilus* compete for space only to a limited extent, and do not constitute serious menaces. Competition by bryozoans is limited.

Summary

1. In March, 1949, nine stations were established in widely separated parts of Apalachicola Bay, Florida. At frequent and regular intervals, salinity, temperature, and oyster spat-fall intensity were checked at these stations. The study ended in December, 1949.
2. Spat-fall occurred from the second week of April until the second week of November.
3. Despite the fact that temperatures sufficient to induce spawning in Long Island Sound were observed in Apalachicola Bay in February, the gonads had scarcely begun to develop at that time. The sex organs did not begin to ripen rapidly until the temperature rose above 20.0°C., during the latter part of February.
4. The first record of isolated spawnings took place at two widely separated parts of the Bay, apparently during the week ending March 30th. The temperatures recorded for that date, at those locations, were 22.5 and 24.0°C.
5. Although a few preliminary spawnings took place, the first mass spawning to occur in Apalachicola Bay in 1949 was during the week ending May 11th. The location was Porter's Bar. The recorded temperature for that date was 26.0°C.
6. In the eastern part of the Bay, mass spawning took place simultaneously at all stations during the week ending June 8th and again in September. The average temperature for all five stations at that time was 28.0°C. At least four other consecutive but not

simultaneous mass spawnings occurred during the spawning season at these stations.

7. In the western part of the Bay spawning was light and not simultaneous with that of the eastern area. This may have been due to lower average temperature with greater fluctuations than in the eastern area.
8. A temperature higher than 25.0°C. is necessary to induce mass spawning. In general 28.0°C. or thereabouts is probably required.
9. Because of the higher mass spawning temperature, it has been suggested that the American oysters indigenous to Florida may be a physiologically different race, or perhaps a subspecies. Without evidence that the physiological differences are inherited, this conclusion cannot be justified. Transplanting Florida oysters to Long Island Sound for study might provide useful information in this respect. On the other hand, a complex interaction of ecological and physiological factors may be responsible for mass spawnings which occur at relatively elevated temperatures.
10. Under normal conditions, and where cultch spreading is well integrated to the reproductive cycle, silting is not a deterrent to setting.
11. Poor condition of oysters is not considered, by itself, a sufficient cause for poor spawning. The oysters of Apalachicola Bay are of extremely low glycogen content, yet produce an enormous amount of spat.
12. In general, the poorest spat-fall occurs in the western part of Apalachicola Bay where most of the commercial harvesting is done.

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GROWTH RATE MEASUREMENT OF SHIPWORMS[1]

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ABSTRACT

Measurements of *Teredo pedicellata* were carried out at Miami Beach during 1949 and 1950 primarily for the purpose of comparing burrow length and body weights as indices of seasonal growth rate fluctuation. Growth was shown to take place most rapidly during midsummer, with a secondary maximum in March. It was noted that in panels exposed for more than two months the summer growth rate was reduced as a result of overcrowding, due to the heavy summer attack rate. The dry weight is shown to vary as the 1.28 power of the burrow length. The approximation to a linear relationship may possibly result from the disproportionately high weight of shell and pallet in smaller animals.

INTRODUCTION

Among previously recorded investigations of marine, wood-boring molluscs, few are concerned, except incidentally, with rate of growth. Other sessile marine invertebrates, such as the barnacles, have received greater attention in this respect. Moore (1934a, 1934b, 1935) developed techniques for measuring the growth of several different species of *Balanus* in various locations. He found volumetric measurements to be a more consistent index of growth than linear measurements. An example of the complications which may arise when linear measurements alone are used is given by a study of growth rate of *Callinectes* in which, because of differential growth of the various body regions, it was necessary to measure five separate linear dimensions (Newcombe, 1948).

Needler (1940) found shipworm growth to be most rapid in Malpeque Bay during the summer. Maximum growth rate coincided with the period of highest temperature, but growth continued, at a lesser rate, even below 10°C. The maximum length attained in one season was about 24 cm. No other factors such as salinity changes were found to be associated with the seasonal cycle in growth rate.

An investigation at Ponce de Leon Inlet, Daytona Beach, Florida, (Richards and Clapp, 1944) showed that the greatest teredid growth during any one month occurred at the time of heaviest attack. There

1 Contribution No. 58 from The Marine Laboratory, University of Miami. These studies were aided by a contract between the Office of Naval Research, Department of the Navy and the University of Miami in cooperation with the U. S. Navy Bureau of Yards and Docks.

were two such maxima, one in the May-June period and one in September. The maximum size recorded at the age of one month was 40 mm. The organisms were principally *Bankia gouldi.*

In the Woods Hole, Massachusetts area, a similar study, which included such diverse forms as *Obelia, Balanus, Hydroides* and *Botryllus,* showed that *Teredo navalis* becomes sexually mature in two months and reaches adult size in one year (Grave, 1933). The same author (1928) found that young teredids ranged in size from 0.35 mm. to 1 mm. at two or three weeks after settling, and from 5 to 7 mm. with a diameter of 2-2.5 mm. at the end of one month. Grave furthermore states that burrow size measurements are a satisfactory index of growth rate in shipworms, without however, offering comparative data from other possible methods of measurement. Observations upon growth of *Bankia gouldi* at Beaufort, N. C., are given by Sigerfoos (1907), whose measurements after periods of growth of twelve days, twenty days, and thirty-six days, were 3 mm., 11 mm. and 100 mm. respectively. This represents a higher growth rate than Richards and Clapp report for the same species in Florida waters, but no exact comparison is possible due to lack of sufficient data regarding variation of growth with age and season.

In the Pacific area similar methods were applied by Kofoid and Miller (1927) in order to measure the boring rates of *Teredo navalis* and *Bankia setacea. Teredo navalis* was found to have an average rate of boring of about 2 cm. per month, while the rate for *Bankia* approximated 4.7 cm. per month. The individual rate of boring was found to vary considerably. On the Pacific coast, Johnson and Miller (1935) reported the largest specimen of *Bankia* at Friday Harbor as 3.9 cm. long. This specimen was from a block which had been exposed for four months from September to January. The average length of the ten largest specimens was 2.54 cm., with a rate of growth of about one cm. per month. The shipworm involved is regarded as a cold water species with maximum attachment from October through December.

Elsewhere in the Pacific a diameter of three-sixteenths of an inch was reported at the end of three months growth of three Australian species of *Teredo* (Johnson, *et al,* 1936). The maximum length attained by some species of teredids is considerably higher than those referred to above. The various accounts which include these do not, however, give any satisfactory estimate of growth rate during the first few months after entrance.

Since 1949 intensive studies of the physiology of marine borers

have been carried out at Miami. In view of this it was considered important to obtain information regarding natural growth rate in this area, for which no previous records are available. It was also considered of value to compare the consistency of burrow length and weight measurements as growth indices.

Acknowledgments are gratefully accorded to Mr. Herman D. Doochin and other members of the Laboratory staff whose help made possible the completion of this study.

Methods

The panels used to collect specimens for measurement were of clear pine, one-half inch in thickness, six inches in width, and 10 inches in length. They were suspended in the sea in open frames about one foot below the surface at low tide. The frames in which the panels were mounted were painted with an anti-fouling paint for protection. This did not seem to affect borer attack on the collecting panels.

Two series of growth rate measurements were undertaken. The first was begun in January 1949 and was based solely upon linear measurements of the burrows. The second series, which was begun in February 1950, included measurements of both burrow length and weight.

In 1949 the collecting panels were suspended in the water in two frames, each containing 12 panels. These frames were hung from a dock at the Miami Beach Boat Slips, where tidal currents and nearby marine structures ensure borer attack. At the end of the exposure period, which varied from one to seven months, a panel was removed from each frame for inspection and measurement of the contained borers.

This series was abandoned in August 1949, when the frames were destroyed by a storm.

In February 1950 a single rack, containing 20 panels, was exposed. This was suspended from the edge of a small dock at the Causeway Terminal Yacht Basin. At this location the tidal currents sweep past the panels and conditions are very similar to those at the location used in 1949. Shipworm attack was encountered during each month of the year in both locations. It was originally intended that 12 panels be exposed and that one of these be examined each month, in order to furnish a series of samples with exposure periods ranging from a month to one year. A similar series of panels was to be exposed for similar periods during successive months of the year. It was found, however, that the panels became so riddled with burrows after five

months exposure that competition for space prevented further growth and killed some of the shipworms. Even in panels exposed for periods of four months many of the larger burrows were empty and furnished no material for growth determination by weight. For this reason the longer exposures were abandoned and observations were restricted to panels exposed for from two to four months. It was found that when panels were exposed for only one month the shipworms were neither large enough nor numerous enough to furnish material adequate for growth rate determination.

In April 1950, and each month thereafter, a panel which had been exposed for two months was removed from the frame. At the end of each month a second panel, exposed for a longer period, was also removed. In most cases this second panel had been exposed for four months, although one was exposed for three, and one for five months. As each panel was removed it was replaced by a fresh panel.

Upon removal from the water, the panels were scraped clean of fouling, and washed in seawater prior to inspection. They were split apart and the specimens removed by carefully cutting away the wood from around the burrows. The lengths of the largest burrows were then measured, and the average of the 10 greatest was recorded. The 10 largest specimens were removed from each panel and placed in individual containers of water. There was usually a lapse of two hours or less between collecting the specimens and weighing them. During this time the specimens were kept cool by refrigeration. Each specimen was removed from its container immediately before weighing and was gently rolled about on filter paper to remove excess moisture. The shipworms were invariably flaccid after removal from the burrows and the experimental procedure appeared to be sufficient to remove all free water from within the mantle cavity. The average wet weights included shells and pallets but not the calcareous burrow lining. After drying overnight in a vacuum oven at 60°C. and *ca.* 1 mm. pressure, the average dry weight was obtained.

Results

The marine borers encountered in this investigation included *Teredo* (*Lyrodus*) *pedicellata* Quatrefages, *Bankia fimbriatula* Moll and Roch, and an unidentified species of *Phyloteredo*. The first named was by far the most numerous, and the only one which was found in every panel inspected. Specimens of *Phyloteredo* were seldom found and *Bankia* was common only during the winter months. For this reason the measurements were confined to *Teredo pedicellata*.

During 1950 the burrow length measurements for varying periods of exposure were compared with wet weight and dry weight measurements (Figure 1). There is a good general agreement between the

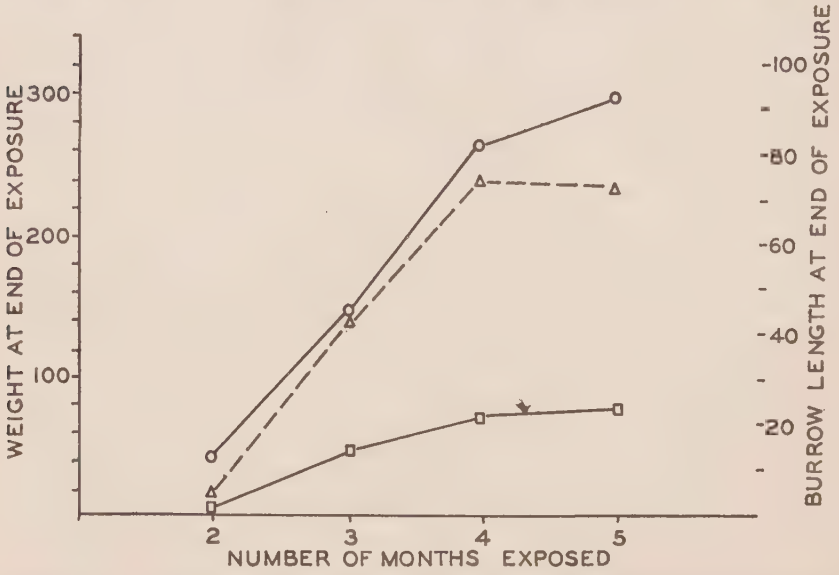

FIGURE 1. Comparison of weight and burrow length measurements with age of *Teredo pedicellata* in panels exposed from February 1950. Circular convention represents burrow length; triangular convention, wet weight; square convention, dry weight.

general trends of the three measurements. Maximum size was reached at the end of five months when the burrow length was 92.5 mm., the dry weight 72 mg. and the wet weight 225 mg. There was a slight apparent loss of wet weight during the fifth month of exposure, although the burrow length and dry weight continued to increase. This is believed to fall within the limits of the sampling error, due to the methods employed.

Measurements of size in relation to age were carried out by exposing a number of panels from the same initial date and removing them at monthly intervals in order to measure the shipworms within them. Thus the measurements were taken from successive different samples of a population rather than from the same individuals at successive intervals. This leads to a variability in the measurements that is not due simply to age. Since the growth at different ages took place at different seasons of the year, the growth curve was also to some extent influenced by seasonal fluctuations.

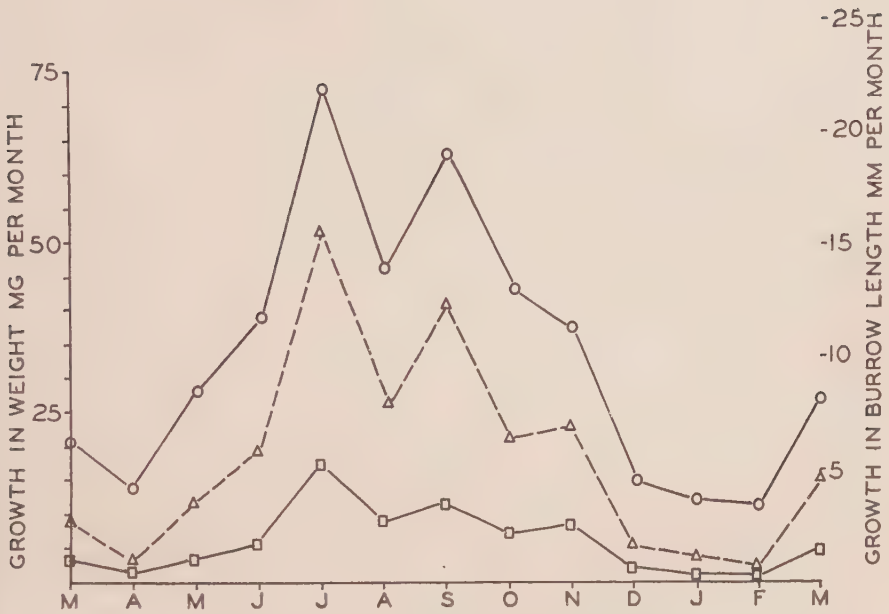

FIGURE 2. Seasonal changes in growth rate of *Teredo pedicellata* from panels exposed for periods of two months during 1950. Observations are plotted at the middle of the exposure period. Conventions as in Figure 1.

Seasonal variation in the growth rate during two month exposure periods in 1950 is shown in Figure 2. All three methods of measurement show similar maxima in June-July and in August-September. A smaller secondary maximum appeared in March. During the July maximum the burrow length increased at the rate of 21.5 mm. per month. The wet weight increased by 52 mg. per month and the dry weight by 18 mg. Observations upon panels exposed for four month periods unexpectedly showed a growth rate maximum in February-May and a smaller one in August-November (Figure 3). During October-January there was an additional maximum in weight increase which was reflected only to a small degree in the curve of burrow length.

DISCUSSION

Observations upon the rate of growth of *Teredo pedicellata* at Miami Beach showed an average monthly maximum of 29.3 mm. per month. No records of the growth rate of this species in other areas

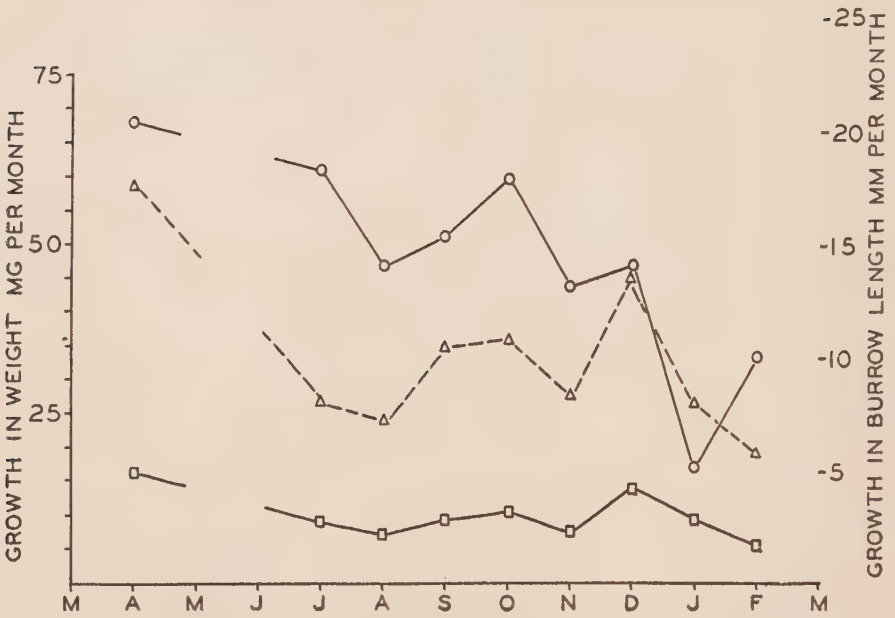

FIGURE 3. Similar to Figure 2 except that panels were exposed for four month periods.

are available for comparison. This is lower than the growth rate of *Bankia gouldi* at Daytona Beach, the nearest locality to Miami at which studies of this nature have been carried out.

In order to investigate the relationship between burrow length and body weight, the logarithmic values of weights may be plotted against logarithmic values of burrow length (Figures 4, 5). The observations from both two-month and four-month panels fit fairly closely to a curve of the type $W = aL^n$, where n is equal to 1.28 for dry weight and to 1.37 for wet weight. Thus the weight does not increase as the approximate cube of the length, as might be expected, but according to a more linear relationship.

The explanation for this relationship may lie in the fact that the proportion of shell (excluding burrow lining) to tissue weight decreases with increasing size. Data communicated by Dr. Charles E. Lane show that the shell weight including pallets constitutes 45 per cent of the dry weight of an individual weighing 2 mg. and that this decreases to 17 per cent in the case of an individual weighing 22 mg. Thus, the body weight would be more closely related to the cube of length if the shell weight were not included. Unfortunately no ob-

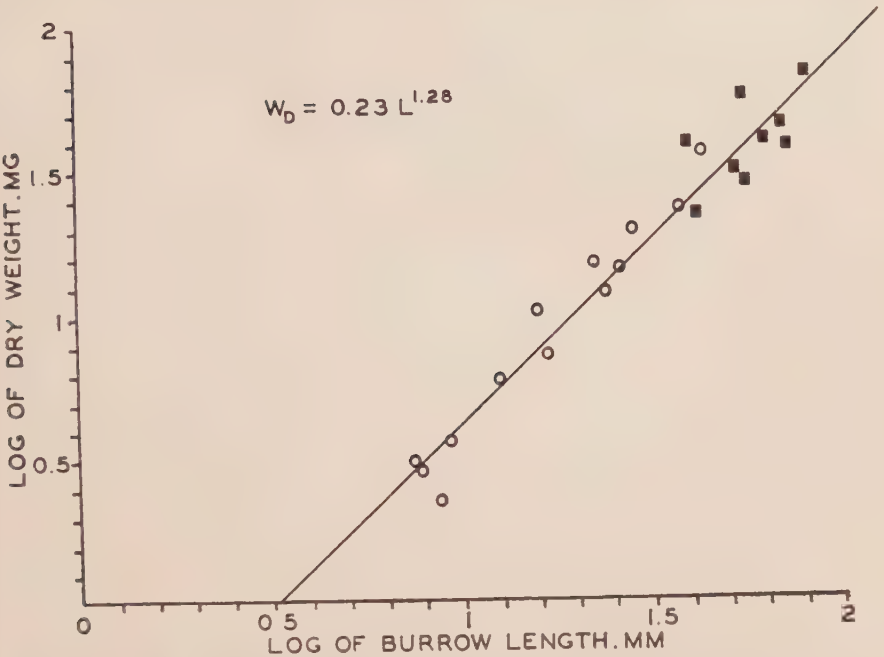

FIGURE 4. The relation between dry weight and burrow length. Both plotted logarithmically.

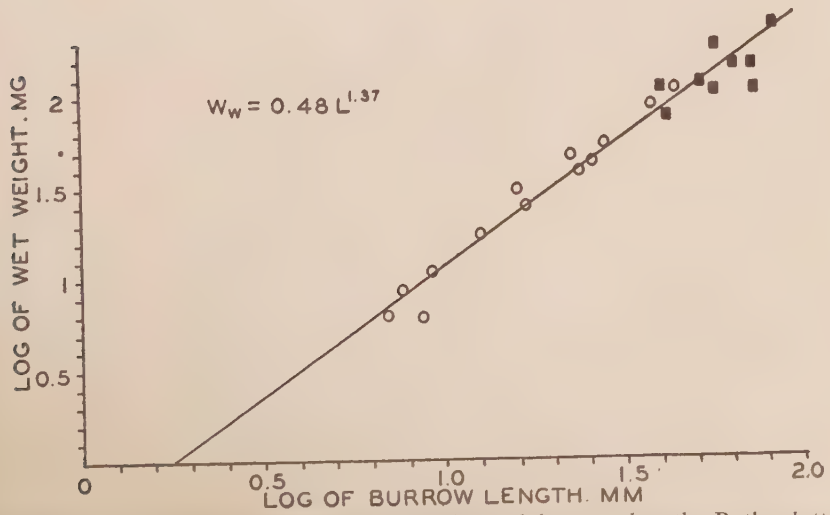

FIGURE 5. The relation between wet weight and burrow length. Both plotted logarithmically.

servations were made with which this might be confirmed.

A comparison of the dry weight/wet weight ratio shows an increase in the ratio with decreasing length. This may be similarly accounted for by the disproportionately large size of the shell and pallets in smaller individuals.

Should further study show changes in shell tissue ratio are insufficient to account for the nature of the length-weight relationship, then the remaining discrepancy would suggest that the worms produce a longer burrow than they are able adequately to fill. This in turn might indicate that the unexpectedly rapid increase of burrow length relative to weight is due to eating the wood for feeding purposes, rather than to providing space for the body. The subject calls for further study, which should take into account the changes in burrow diameter as well as length, and which should consider tissue weight separately from shell weight.

The seasonal fluctuations in growth rate at Miami Beach show a summer maximum similar to that observed in most other locations previously investigated. There is in addition, however, a secondary maximum in March. This does not appear to occur at Daytona Beach, about 200 miles to the north, and is probably associated with the higher winter seawater temperatures at Miami.

Four-month panels were observed to have a somewhat different seasonal fluctuation from that of the two-month panels. The summer maximum was less pronounced and the winter or spring maximum more marked. This may be due to the overcrowding which occurred in panels subjected to more lengthy exposure. This would be further emphasized during the summer months by the greater summer growth rate. At this time the intensity of attack is greatest, so that in a period of less than four months the wood is heavily riddled with burrows and further extension in burrow length must be seriously interfered with. The maximum growth in two month panels occurred during July to September, whereas, in the four-month panels, the overcrowding may have reduced summer growth somewhat below what it would otherwise have been. During April the lack of crowding would allow unimpeded growth. Thus, in four-month panels, the spring growth maximum would reach a higher level relative to the summer maximum than was the case in the uncrowded two-month panels.

In order to test this hypothesis a comparison of growth rate with the degree of crowding was effected. Use is made in Table I of a numerical expression for crowding which is based upon the number of new borings counted in a standard test panel at the end of each

TABLE I

EFFECT OF CROWDING UPON GROWTH OF SHIPWORMS IN PANELS EXPOSED FOR TWO MONTH PERIODS DURING 1950

MONTH PLACED ON EXPOSURE	ATTACK RATE FIRST MONTH	ATTACK RATE SECOND MONTH	CROWDING INDEX $\frac{5.2I_1 + 1.6I_2}{100}$	CUBE OF BURROW LENGTH $L^3/100$
March	93	25	5	6
April	25	211	5	47
February	(93)	93	(6)	43
December	107	(107)	(7)	4
January	(107)	(93)	(9)	3
August	130	381	13	540
November	227	(107)	(14)	8
July	269	130	16	220
May	211	948	26	130
September	381	628	30	180
October	628	227	36	115
June	948	269	54	812

Attack rates shown in parentheses are estimates for months when complete data were unavailable.

month in the year. These data were kindly supplied by Mr. Leonard J. Greenfield who made the observations as part of a separate investigation. The new borings which occurred during the second month of exposure were free to grow for an average period of ½ month. The attack rate was therefore weighted by half the growth occurring during the first month of life, using the data from which Figure 1 was compiled. Similarly, the attack rate of the first month of exposure was weighted by the growth which occurs during the first 1½ months. This is the average time remaining for growth in the case of shipworms entering during the first month of a two-month exposure period.

The sum of the weighted attack rates was used as an index of crowding. This is ranged in descending order of magnitude. A comparison of the crowding index and size in terms of the cube of burrow length shows that there is no retardation of growth with increasing crowding but rather that the periods of high attack rate and high seasonal growth rate coincide. The growth in two-month panels is therefore considered a suitable measurement for defining seasonal fluctuation, uncomplicated by the effects of crowding.

In order to determine the effects of crowding in four-month panels, a similar crowding index was calculated. In this case the attack rates of the first two and the last two months were weighted by the growth measured in four- and two-month panels exposed during the same season.

The growth in four-month panels is expressed as a multiple of that

TABLE II

EFFECT OF CROWDING UPON GROWTH OF SHIPWORMS IN PANELS EXPOSED FOR TWO MONTH PERIODS DURING 1950

MONTH EXPOSED	ATTACK RATE FIRST 2 MONTHS I_2	ATTACK RATE SECOND 2 MONTHS I_4	CROWDING INDEX $(I_2L_4 + I_4L_2)/100$*	RATIO OF GROWTH IN TWO AND FOUR MONTH PANELS $(L_4/L_2)3$**
December	(214)	(186)	(102)	205
November	(344)	(200)	(152)	149
February	(186)	236	183	857
July	399	1009	376	4
October	855	(214)	(535)	227
September	1009	(334)	(616)	12
August	511	855	689	20
June	1217	511	909	8
May	1159	399	938	5

*L_2 and L_4 for coincident initial dates of exposure.
**L_2 and L_4 for coincident mid-period dates of exposure.
Attack rates shown in parentheses are estimates for months when complete data were unavailable.

in the corresponding two-month panels. The latter has already been shown to be undiminished by crowding. The ratio is therefore an expression of the effects of crowding in four-month panels uncomplicated by seasonal variation in growth. It is clear from the tabulated data that there is a considerable decrease of growth in the four-month panels as the crowding index increases. Thus it is apparent that after two months of exposure there is a strong tendency for crowding to reduce the rate of growth and so to obscure seasonal growth fluctuation.

The basis for calculating the crowding index obviously does not satisfy all theoretical requirements. A more satisfactory basis of calculation from this standpoint would be considerably more complicated and probably not justified by the limitations of the raw data. The relations between growth and the crowding index in both sets of panels were nevertheless generally borne out, when crowding was expressed in a number of alternative ways including the unweighted attack rate. It is therefore considered that the crowding effect discussed above is reasonably well established.

From the above discussion it becomes clear that in areas subjected to heavy attack the use of growth rate data in ecological studies must be limited to observations on panels exposed for periods of no more than two months, in order to avoid the effects of crowding. Thicker timber than used in these experiments, although less subject to the effects of crowding, is not suitable for growth rate studies because of the difficulty of extracting whole organisms. It is also clear that

growth in burrow length and in body weight are not closely dependent upon each other, although both show the same general seasonal fluctuations.

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CONTRIBUTIONS will be considered which deal with research in the marine sciences, directly or indirectly related to the southeastern United States and the Caribbean area. Papers dealing solely with the economic or applied aspects of commercial fisheries will not be accepted.

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Bibliographical references must be indicated by author's name and year of publication. References should be listed under that heading in alphabetical order of authors. Each reference should include the last name followed by initials or the first name. Co-authors should be listed with initials preceding the last name. The date should appear next to the author's name, followed by a complete title, in lower case except for the first word. The publisher, city and pagination should follow, in the case of books. The names of periodicals should be abbreviated as in "World List of Scientific Periodicals," Oxford. The volume is then given in arabic numerals underlined for italics, followed by the number in brackets and the pagination preceded by a colon. After the first line of each reference the copy is indented.

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TABLE OF CONTENTS

PAGE

1. JOHN B. LEWIS: The phyllosoma larvae of the spiny lobster *Panulirus argus* 89

2. C. E. LANE and J. Q. TIERNEY: Hydrodynamics and respiration in *Teredo* 104

3. ROBERT M. INGLE: Spawning and setting of oysters in relation to seasonal environmental changes 111

4. LAWRENCE B. ISHAM, HILARY B. MOORE and F. G. WALTON SMITH: Growth rate measurement of shipworms 136